Tree Genetics & Genomes (2016) 12: 25
DOI 10.1007/s11295-016-0985-z

ORIGINAL ARTICLE

QTL mapping and breeding value estimation through pedigree-based analysis of fruit size and weight in four diverse peach breeding programs

Jonathan Fresnedo-Ramírez[1,2] · Terrence J. Frett[3,4] · Paul J. Sandefur[3,5] · Alejandra Salgado-Rojas[3] · John R. Clark[3] · Ksenija Gasic[4] · Cameron P. Peace[5] · Natalie Anderson[6] · Timothy P. Hartmann[6] · David H. Byrne[6] · Marco C. A. M. Bink[7] · Eric van de Weg[8] · Carlos H. Crisosto[1] · Thomas M. Gradziel[1]

Received: 2 July 2015 / Revised: 13 December 2015 / Accepted: 3 March 2016 / Published online: 17 March 2016
© Springer-Verlag Berlin Heidelberg 2016

Abstract The narrow genetic base of peach (*Prunus persica* L. Batsch) challenges efforts to accurately dissect the genetic architecture of complex traits. Standardized phenotypic assessment of pedigree-linked breeding germplasm and new molecular strategies and analytical approaches developed and conducted during the RosBREED project for enabling marker-assisted breeding (MAB) in Rosaceae crops has overcome several aspects of this challenge. The genetic

Communicated by C. Dardick

Electronic supplementary material The online version of this article (doi:10.1007/s11295-016-0985-z) contains supplementary material, which is available to authorized users.

✉ Thomas M. Gradziel
tmgradziel@ucdavis.edu

Jonathan Fresnedo-Ramírez
jfresnedo@cornell.edu

Terrence J. Frett
tjfrett@email.uark.edu

Paul J. Sandefur
paul.sandefur@email.wsu.edu

Alejandra Salgado-Rojas
asalgado@email.uark.edu

John R. Clark
jrclark@uark.edu

Ksenija Gasic
kgasic@clemson.edu

Cameron P. Peace
cpeace@wsu.edu

Natalie Anderson
n-anderson@tamu.edu

Timothy P. Hartmann
guero_ag05@neo.tamu.edu

David H. Byrne
dbyrne@tamu.edu

Marco C. A. M. Bink
marco.bink@wur.nl

Eric van de Weg
eric.vandeweg@wur.nl

Carlos H. Crisosto
chcrisosto@ucdavis.edu

[1] Department of Plant Sciences, University of California, Davis, CA 95616, USA

[2] Present address: BRC Bioinformatics Facility, Institute of Biotechnology, Cornell University, Ithaca, NY 14853, USA

[3] Department of Horticulture, University of Arkansas, Fayetteville, AR 72701, USA

[4] Department of Agricultural and Environmental Sciences, Clemson University, Clemson, SC 29634, USA

[5] Department of Horticulture, Washington State University, Pullman, WA 99164, USA

[6] Texas A&M University, College Station, TX 77843, USA

[7] Biometris, Wageningen University and Research Centre, P.O. Box 16, 6700 AA Wageningen, The Netherlands

[8] Wageningen UR Plant Breeding, Wageningen University and Research Centre, PO Box 386, 6700 AJ Wageningen, The Netherlands

underpinnings of fruit size (fruit equatorial diameter (FD)) and weight (fresh weight (FW)), two most important components of yield, were investigated using the pedigree-based analysis (PBA) approach under a Bayesian framework which has emerged as an alternative strategy to study the genetics of quantitative traits within diverse breeding germplasm across breeding programs. In this study, a complex pedigree with the common founder "Orange Cling" was identified and FD and FW data from 2011 and 2012 analyzed. A genetic model including genetic additive and dominance effects was considered, and its robustness was evaluated by using various prior and initial values in the Markov chain Monte Carlo procedure. Five QTLs were identified which accounted for up to 29 and 17 % of the phenotypic variation for FD and FW, respectively. Additionally, genomic breeding values were obtained for both traits, with accuracies >85 %. This approach serves as a model study for performing PBA across diverse pedigrees. By incorporating multiple breeding programs, the method and results presented support and highlight the ability of this strategy to identify genomic resources as targets for DNA marker development and subsequent MAB within each program.

Keywords *Prunus persica* (L.) Batsch · Breeding germplasm diversity · "Orange Cling" · Complex traits · Dominance

Introduction

Quantitative trait loci (QTL) mapping has been pursued for many years by numerous research groups in efforts to better understand the genetic control of complex fruit-crop traits. Although peach (*Prunus persica* (L.) Batsch) exhibits substantial phenotypic variability, it suffers from restricted genetic diversity resulting from extensive inbreeding (Font i Forcada et al. 2012) and significant genetic bottlenecks during its domestication and subsequent breeding (Gradziel et al. 1993; Scorza et al. 1985). Nevertheless, advances in the understanding of the genetic control of several traits have taken place in the last 20 years, making peach the model species for fruit crops in the Rosaceae (Shulaev et al. 2008). To date, numerous QTL studies have been performed in peach (Eduardo et al. 2011; Etienne et al. 2002; Fan et al. 2010; Quilot et al. 2004; Yamamoto et al. 2001; Zhebentyayeva et al. 2008), yet the conversion of these QTLs into DNA tests and their subsequent adoption by breeders for use in marker-assisted breeding (MAB) has been limited (Byrne et al. 2012). Furthermore, all studies incorporated bi-parental or pseudo-testcross populations, and therefore may have underrepresented the genetic components of these traits in ongoing breeding programs (Peace et al. 2014). Therefore, the relevance of these findings may be limited to specific breeding germplasm.

Pedigree-based analysis (PBA; Bink et al. 2008; 2014) has arisen as an innovative, alternative QTL mapping approach which simultaneously incorporates the use of multiple small populations connected in a pedigree to enhance the identification of important QTLs whose alleles segregate for a trait in or across breeding programs. The PBA mapping approach facilitates the calculation of genetic parameters such as heritability, additive and dominance variances and breeding values, and tracks filial relationships through several generations of the pedigree. Thus, PBA genetic estimates can have a higher degree of certainty, even for those components with only moderate effects (Jannink et al. 2001). Additionally, incorporating a more extensive and diverse genetic background into QTL analysis increases mapping resolution and allele segregation, which ultimately enhances the ability to detect full QTL action for the trait of interest (Yu and Buckler 2006).

Because complex trait improvement is often a major focus of breeding programs, the accurate genetic dissection of such traits is essential. The most investigated complex trait in crops is yield (Shi et al. 2009). The most common method for disentangling yield and other complex traits has been through QTL mapping (Bai et al. 2012; Fanizza et al. 2005; Lacape et al. 2013; Peng et al. 2011; Portis et al. 2014; Quarrie et al. 2006; Semel et al. 2006). Yield improvement is often pursued through advances in understanding and manipulation of key determinants such as early fruit cell division and subsequent development (Lippman and Tanksley 2001). Such determinants are typically controlled by a combination of additive, dominance (Semel et al. 2006) and epistatic (Zdravkovic et al. 2000) genetic effects. The Mendelian factors involved in complex traits can be identified and characterized to support and direct breeding decisions (Paterson et al. 1988), such as candidate genes for cell number regulator (*CNR*) in peach, which have recently been located within QTL regions related to *Prunus* fruit size in sweet and sour cherry (De Franceschi et al. 2013).

The PBA approach for mapping QTLs using linkage methods within pedigrees was employed by the recent RosBREED-I initiative (www.rosbreed.org; Iezzoni 2010). By using markers developed through the IPSC 9K peach SNP array v1 (Verde et al. 2012a), this approach permitted tracking alleles identical by descent for QTL analysis within a Bayesian framework. The approach also allowed estimation of genetic variances and genomic breeding values for different accessions while also providing additional genetic information (Bink et al. 2008). Studies using the PBA Bayesian strategy have been performed in apple (Bink et al. 2014) and cherry (Rosyara et al. 2013) and in a peach pedigree containing genetic introgression from related species (Fresnedo-Ramírez et al. 2015a).

For the breeding of perennial fruit tree crops, the development of large, complex-trait-segregating bi-parental populations is uncommon due to long juvenility periods, space limitations, and high costs for generation and maintenance of such populations. Without such populations, the dissection of traits in order to reveal and understand their underlying

genetic components cannot be completed using standard QTL mapping approaches. Therefore, the application of PBA, which fits into the logistics of fruit tree breeding where the individual is the selection unit, homozygous lines are not created, the breeding cycle is long, overlapping across generations within the breeding program, and population sizes are usually small, will aid in the identification of those genetic components that pedigree-connected germplasm share. The incorporation of PBA is desirable for crops with narrow genetic bases, such as peach, as well as when data is available from several breeding programs with pedigree-connected germplasm (Peace et al. 2014). Thus, geneticists can target the dissection of such common genetic components of complex traits and aid breeders in the development of DNA tests targeting genomic regions of relevance across breeding programs. Such DNA tests will be useful for marker-assisted selection of parents and seedlings across several breeding programs, simultaneously.

This study aims to identify the genetic components of fruit equatorial diameter (FD) and fruit fresh weight (FW) shared, as well as differences of these components, across peach germplasm used in four US breeding programs. Both FD and FW are components of yield, a complex trait of direct breeding relevance with an already extensively developed scientific framework. QTLs for FD and FW have been identified through the use of bi-parental segregating populations, either using intraspecific germplasm sets of peach (da Silva Linge et al. 2015; Eduardo et al. 2011) or interspecific crosses having a peach cultivar as parent (Quilot et al. 2004) and in *Prunus*-related species such as almond (Fernández i Martí et al. 2013). However, these QTLs have not been validated in breeding-relevant germplasm. Deploying PBA on germplasm from four breeding programs sharing ancestry and optimizing the strategy presented by Peace et al. (2014) for exploiting the representation of important breeding parents with high average allelic representation represents a step forward in the validation of QTLs in a diverse breeding germplasm. This PBA approach is thus crucial to develop breeding-relevant DNA tests for broad application of marker-assisted selection in and across peach breeding programs.

The present work shows the framework developed to characterize genetic components controlling FD and FW in peach using the PBA on a broad pedigree tracing back to the landmark cultivar “Orange Cling” (syn. “Orange Clingstone”) and spanning four public breeding programs: Clemson University, the University of Arkansas, the University of California at Davis, and the Texas A&M University. Orange Cling, dating back to the early 19th century in the USA (American Pomological Society and Ragan 1899; Hedrick et al. 1917), was identified as a main founder in the diverse pedigree used in this study. This cultivar also provided the most genotypic and phenotypic data in its lineages, which also possesses contributions from several cultivars and breeding selections for both fresh consumption and processing peach types. In addition to direct analysis of breeding data, this study presents a framework and recommendations to optimize the dissection of relevant complex traits across breeding programs. Such a strategy should facilitate the generation of functional DNA tests and so aid the development of superior cultivars. This is the first attempt for dissection of complex traits across breeding programs of stone fruit tree crops and is based on the data generated and available through the RosBREED project. The framework developed here will aid the analysis for relevant complex traits across multiple Rosaceae breeding programs in the newly funded RosBREED project, FruitBreedomics (www.fruitbreedomics.com), as well as similar collaborative projects.

Materials and methods

Phenotypic and genotypic information

Measurement of FD in millimeters and FW in grams was taken over 2 years (2011 and 2012) following an established peach standardized phenotyping protocol (Frett et al. 2012). The genotypic information was generated as part of the RosBREED project (Iezzoni 2010) using 2398 single nucleotide polymorphisms (SNPs) derived from the IPSC 9K SNP array for peach (Verde et al. 2012a), as well as four simple sequence repeat markers (SSRs: BPPCT015, CPPCT040, endoPG.1, and endoPG.6) that were used as quality control markers for amplification during the genotyping of the RosBREED peach set and subsequently for parentage verification during genetic analysis.

Pedigree identification

The germplasm used in this study was a subset of the RosBREED germplasm, chosen to effectively represent alleles currently found within North American peach breeding germplasm (Peace et al. 2014). Important breeding pedigrees for processing (Gradziel et al. 1993) and fresh market (Scorza et al. 1985) cultivars were identified and integrated in a comprehensive pedigree of 1819 individuals including 747 accessions that were not genotyped or phenotyped, 867 progenies comprising a series of breeding populations from the four breeding programs, and 205 phantom parents (used to avoid semi-founders and so provide an equilibrated pedigree for analysis). The distribution of breeding selections per breeding program was as follows: 210 were from the breeding program at Clemson University, 142 from the University of Arkansas, 240 from the University of California at Davis, and 275 from Texas A&M University. This pedigree was unbalanced and had several gaps in phenotypic and genotypic records that limited the traceability of filial relationships. After maximizing

traceability, only 724 individuals possessed phenotypic records for FD and FW in both 2011 and 2012. Consequently, an initial challenge was to identify a highly informative pedigree with accessions possessing phenotypic and genotypic records across several generations. The filial relationships within families within the RosBREED peach germplasm were checked and corrected using a set of four simple sequence repeats (SSRs) targeting the endoPG locus (Peace et al. 2005) and 450 robust SNPs from the IPSC 9K SNP array for peach (Verde et al. 2012a). In the case of University of California at Davis program, an additional correction was performed as showed by Fresnedo-Ramírez et al. (2015b).

The routines bitSize and pedigree.shrink from the kinship2 package (Therneau et al. 2013) of R environment for statistical computing version 3.0.1 (R Core Team 2013) were applied to each pedigree founder within the pedigree set, to establish a preliminary pedigree derived from the heirloom cultivar Orange Cling. The resulting preliminary pedigree integrated 598 individuals and a maximum generation coefficient of 6.11. To optimize the information from this pedigree, a shrinkage was performed using PediMap 1.2 (Voorrips et al. 2012).

Linkage map

Out of the 2398 SNPs chosen from the IPSC 9K peach SNP array (Verde et al. 2012a), 890 SNPs and four SSR (BPPCT015, CPPCT040, endoPG.1, and endoPG.6) markers were polymorphic with a segregation distortion of no more than 1 % within the selected pedigree and no more than 5 % missing data within the 867 progenies selected for linkage map development. The selected SNPs were subsequently checked through marker consistency check routines available in FlexQTL™ version 0.99112 (Bink et al. 2008, 2014).

Because the PBA framework and FlexQTL™ required the definition of a "parameter space" (search space) for the positions of putative QTLs during the MCMC simulation and a consensus RosBREED linkage map for peach was not yet available, we developed a genetic map based on predictions of genetic distances, incorporating the physical and genetic positions of 68 markers included in the *Prunus* bin map on the Genome Database for Rosaceae (GDR; Cabrera et al. 2009; Howad et al. 2005; Zhebentyayeva et al. 2008). The estimation of genetic distances using polynomial equations was used rather than a simple static conversion factor, because it gave a constant recombination rate for all linkage groups and along linkage groups.

Using polynomial least squares curve fitting, we obtained a polynomial equation $y = a_0 + a_1x + a_2x^2 + \ldots + a_jx^j = \sum_{k=1}^{j} a_kx^k$, per linkage group, where a_0 is the intersection with the abscise to the origin (a genetic distance of zero centiMorgans (cM)), y is the genetic distance as a function of the physical position of the marker (x), and a is the coefficient that best fits the data contained in the *Prunus* bin map. Subsequently, we extrapolated genetic distances for the molecular markers based on their physical positions according to the Peach Genome Reference Sequence version 1 (Verde et al. 2013). Selection of the most appropriate equation for each linkage group was performed using the package MASS version 7.3–29 (Venables and Ripley 2002) for the statistical language and environment R 3.0.1 (R Core Team 2013), considering the following criteria: positive Akaike information criterion (AIC) values calculated by the routine stepAIC; positive genetic distances; and a curve tendency similar to the cytological description of the chromosomes (i.e., acrocentric, metacentric, or sub-metacentric) as described by Jelenkovic and Harrington (1972). The goal of using this technique was to maintain the cytological correspondence of the position of the mapped QTLs.

Genetic structure

Genetic structure was characterized for 867 individuals by analyzing their genotypic (2398 SNPs) and phenotypic information (FD and FW in 2011 and 2012) through factor analysis for mixed data (FAMD; Abascal et al. 2006), using library FactoMineR 1.25 (Le et al. 2008) implemented in R 3.0.1 (R Core Team 2013). Three coordinate dimensions were chosen to develop a 3D scatterplot of the results. The application of FAMD enabled maintenance of the original scales and allelic combinations, which were considered categorical data.

Conclusions on the genetic structure of the analyzed germplasm were drawn from the results, with each individual assigned to one of the groups distinguished in the analysis. This assignment was recorded as a covariate (group) that was subsequently integrated into the data file entered in FlexQTL™ (Bink et al. 2008, 2014).

QTL mapping

The phenotypic values per trait per accession were arranged in a normally distributed vector (y) and fit to the regression model $y \sim N(1\mu + \mathbf{Wa} + \mathbf{Zd}, \sigma_e^2)$, in which: μ is the overall mean of the trait; **a** is a vector for regressions on the QTL covariates for additive genetic effects; **W** is a design matrix that links the QTL and effects to the observed phenotypes (including the effect given by genetic structure, which was a uniformly distributed prior); **d** is a vector for regressions on the QTL covariates for dominance genetic effects; and **Z** is a design matrix that links the QTL and effects to observed phenotypes.

Vectors **a** and **d** were assumed (and taken as priors) to be normally distributed, i.e., $\mathbf{a} \sim N(0, \mathbf{I}\sigma_A^2)$ and $\mathbf{d} \sim N(0, \mathbf{I}\sigma_D^2)$, as is the residual error of the model $[e \sim N(0, \mathbf{I}\sigma_e^2)]$, in which σ_A^2 and σ_D^2 are the additive and dominance genetic variances

explained per QTL and σ_e^2 is the residual variance. All variances were estimated using inverse gamma distributions as priors. The fit of the regression model into the Bayesian framework of PBA was performed according to Bink et al. (2014), adding **d** and σ_D^2 to the θ function, which corresponds to a set of unknown model parameters.

For posterior sampling by simulation, Markov chain Monte Carlo (MCMC) simulations of one million iterations for each trait with priors 1, 3, and 5 QTLs were performed, until at least 100 effective chain samples (ECS) for μ, σ_e^2, the number of QTLs (N_{QTL}), and the variance of the number of QTLs (vQTL) were obtained (Sorensen and Gianola 2002). Marker information, skipping, and thinning, corresponded to a thousandth of the length of the MCMC chain; thus, 1000 samples per trait per year were stored and available for subsequent inferences.

Determination of N_{QTL} was based on its statistical evidence, i.e., the value of twice the natural logarithm of its Bayes factor ($2ln$(BF)) (Kass and Raftery 1995), on the Bayes factors of pairwise model comparisons and on the amount of variance explained by those genetic models. For determination of N_{QTL} influencing the traits, the evidence threshold was set as at least positive ($2ln(\text{BF}) > 2$), as considered by Bink et al. (2014). Furthermore, the genetic additive variance explained by all putative QTLs introduced in the most convergent and stable genetic model was estimated.

Values for broad-sense (H^2) and narrow-sense heritability (h^2) were calculated using the values of phenotypic variance (σ_P^2) and σ_e^2 for each trait, and the weighted additive variance of the trait $\left(\overline{\sigma_A^2}\right)$, for the genomic regions with strong evidence for being a QTL, making it equivalent to σ_A^2. Note that the genetic variance is determined by the genetic structure in the germplasm, and the variance explained by the joint genetic action of the additive and dominance effects of the QTLs, since weighted additive and dominance genetic effects $\left(\overline{\sigma_A^2} \text{ and } \overline{\sigma_D^2}, \text{ respectively}\right)$ were considered.

Given that this study is an application of PBA through the Bayesian framework (Bink et al. 2008, 2014), the genetic models were fit through FlexQTL™ version 0.99112. Chromosomal locations were identified based on their evidence value. Subsequently, visual inspection of the trace plots for convergence and stability of the genetic models evaluated per trait was performed to determine reliable QTLs. The main criteria to determine major QTLs per trait included explanation of at least 5 % of the phenotypic variation, exhibition of the QTL with at least positive evidence ($2ln(\text{BF}) > 2$), and probability of >0.50 for both years on the same linkage group (G), while additionally being co-localized within ±5 cM to the region with the highest QTL intensity identified in 2011 (the first year with phenotypic records). The QTLs were named following the GDR format (Jung et al. 2008, 2014).

Genomic breeding values

The a posteriori PBA outcomes were the genomic breeding values (GBVs). Using PostFlexQTL™ version 0.99110, GBVs per individual were obtained for chromosome segments with at least positive QTL evidence, calculated using the 1000 samples analyzed and stored from the MCMC simulations, per trait and per year, as reported by Bink et al. (2014). Prediction accuracy was calculated as the correlation between GBVs and observed values per trait per year. Quantiles for 90, 95, and 97.5 % were obtained through the function quantile in the package stats from R 3.0.1 (R Core Team 2013) using the algorithm type 9, which provides approximately unbiased estimates when the vector of values is normally distributed.

Results

Pedigree identification

A pedigree of 464 individuals (out of the initial 598), possessing maximum genetic and phenotypic information, was selected based on pedigree shrinkage through PediMap 2.1 (Voorrips et al. 2012) and the application of the routines of the package kinship2 (Therneau et al. 2013). This pedigree consisted of 87 founders (individuals for which parentage was unknown), 99 breeding lines and commercial cultivars, 26 phantom parents (which were added to avoid semifounders and balance the pedigree), and 250 progenies. The maximum generation coefficient of the pedigree was 5.52, arranged across 7 generations for which 754 potential informative meioses (377 × 2) were available. A common cultivar founder was Orange Cling, with additional strong contributions from important old cultivars such as "Alameda," "Australian Muir," "Babcock," "Early Crawford," and "Paloro." The optimized pedigree emphasizes the offspring from the historically important Orange Cling (Fig. 1). The details about the number of progenies and relevant cultivars contributed by each breeding program are provided in Online Resource 1.

Across the pedigree, the traits tended to be normally distributed over the 2 years. However, the full sib families were small, being between 13 and 35 individuals, from which the distributions of traits within families were truncated.

Genetic map

Interpolating the genetic distances for a linkage map containing the 2398 SNPs genotyped for the RosBREED's germplasm reference set yielded eight equations, one for each linkage group (Online Resource 2). Out of the 2398

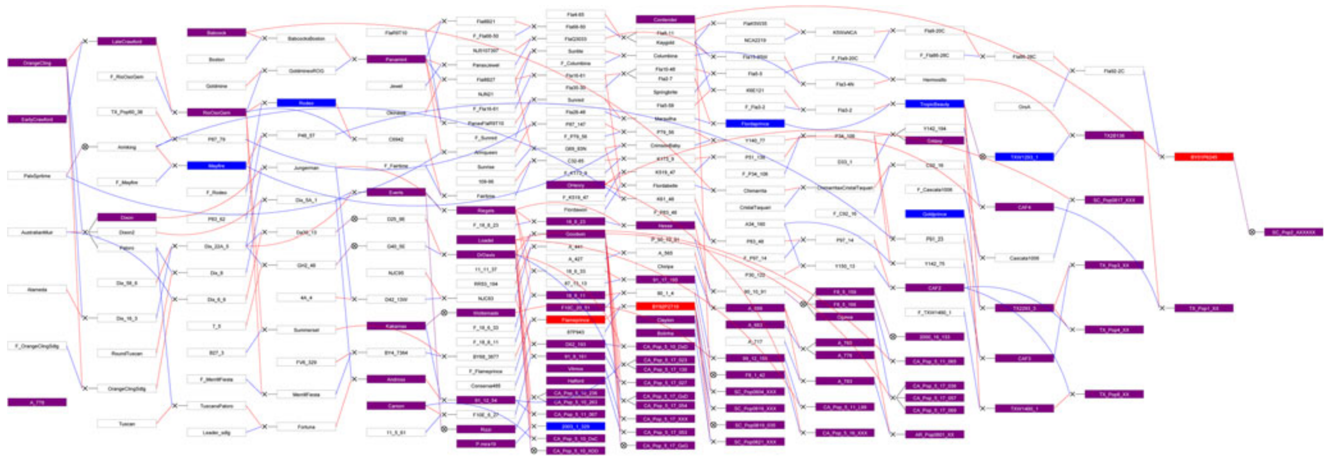

Fig. 1 Summarized pedigree used in this study. Progenies are shown in *one box* only. In *purple*, individuals with phenotypic and genotypic information; in *blue*, individuals with genotypic information only; in *red*, individuals with phenotypic information only. *Blank boxes* represent individuals with missing data for both genotypic and phenotypic data

original segregating SNPs, 890 (37.3 % of the total of SNPs used for genotyping), plus the four SSRs screened, were identified as polymorphic, informative, and having no more than 5 % missing data and 1 % observed genotypic errors within the 250 progenies studied. These SNPs were used to construct the first RosBREED consensus linkage map for peach (referred to as the RC^1 linkage map). The 68 markers from the *Prunus* bin map (reference map) were used as anchors to allocate the 890 SNPs and four SSRs along each linkage group (Fig. 2). Upon completion, the RC^1 linkage map contained 894 markers spread over 8 linkage groups, representing the 8 peach chromosomes, and covering a total genome-wide genetic distance of 491 cM with an average distance between markers of 0.55 cM (Fig. 2). All of the linkage groups (G) covered between 96.97 and 99.60 % of the physical size of the peach chromosomes, and the number of markers mapped on each linkage group ranged from 163 on G4 to 58 on G5 (Table S1 and Figure S1 in Online Resource 2). The longest observed gap between markers was 12 cM at the end of G5.

Genetic structure

The genetic structure identified for the 867 progenies in the RosBREED pedigree showed that the germplasm clustered into groups related to the "stone-adhesion/flesh-texture" trait (Fig. 3). One cluster included clingstone-non-melting accessions (group 1), while the other included primarily freestone-melting accessions (group 2).

QTL mapping and genetic parameters

The QTL mapping showed that while MCMC chains of one million iterations were performed, the convergence for stationary results within an acceptable error may be achieved with as few as 500,000 iterations while keeping 100 samples for statistical inference.

The locations and statistical values of QTLs for FD and FW evaluated in 2011 and 2012 are depicted in Table 1. For FD and FW in both years of the study, the genetic model in which two to three QTLs influence exhibition of each trait showed the

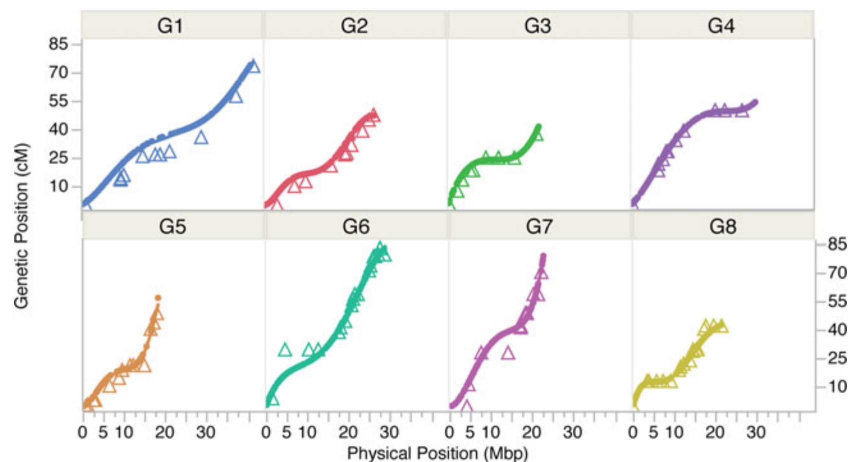

Fig. 2 Allocation of the 2398 SNP markers (*dots*) along the 8 linkage groups of peach based on the location of 68 markers from the *Prunus* bin map (*triangles*)

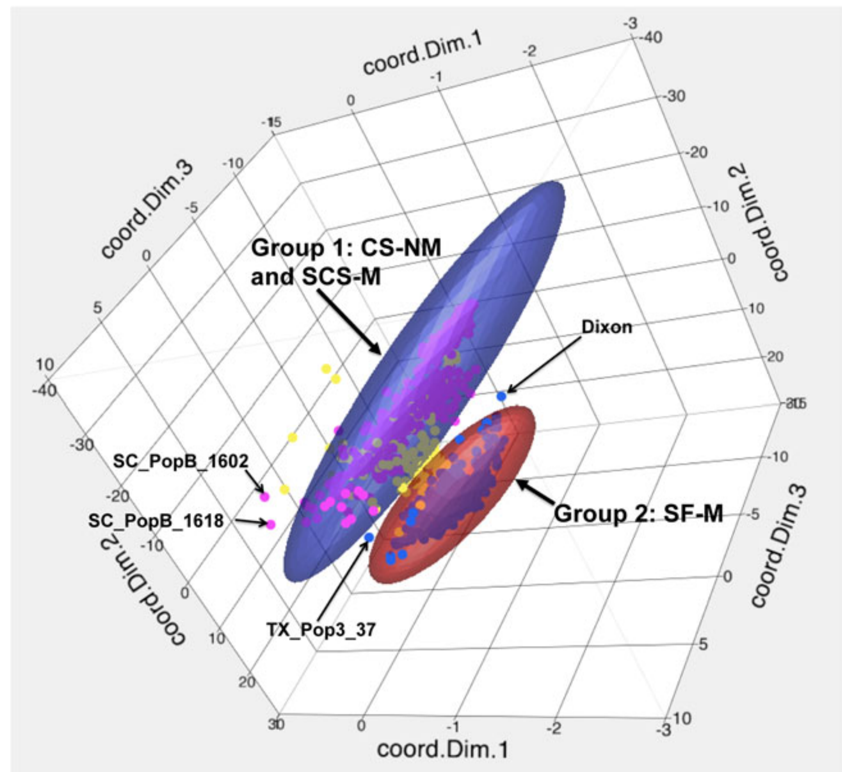

Fig. 3 Genetic structure of the pedigree studied, based on seed adhesion and flesh texture qualities. Group 1 includes clingstone-non-melting (*CS-NM*) and semi-clingstone-melting (*SCS-M*) accessions; Group 2 includes freestone-melting (*SF-M*) type accessions

highest Bayes factors, having positive evidence ($2 \geq 2ln(\text{BF}) \leq 5$). From our analysis, 19 genomic regions across four linkage groups were identified as putative QTLs influencing FD and FW; however, only 5 of those regions showed positive evidence and probability greater than 0.50, supported through visual inspection of trace plots.

The broad-sense heritability (H^2) was between 0.63 and 0.83 for both traits and years; thus, the average H^2 for FD was 0.73 and for FW was 0.72 (Table 2). In comparison, the narrow-sense heritability (h^2) was much lower, between 0.15 and 0.35, with a biannual average of 0.25 for FD and 0.20 for FW. The dominance genetic effects (σ_D^2) explained 3 % of the σ_P^2 for FD in 2011 and 0 % in 2012. Likewise, the FW followed the same decreasing pattern between consecutive years for FD. The σ_D^2 for FW in 2011 explained 4 % of observed phenotypic variation (σ_P^2), yet only 1 % in 2012 (Table 2).

The priors used for N_{QTL} clearly influenced the number of putative QTLs and their evidence for both traits and years (Table 1). When larger values for the N_{QTL} were used, less QTLs with positive evidence were identified. However, on average, chromosomal locations for QTLs influencing FD and FW were identified in both years, with co-localization of the QTL regions influencing both traits. The location and average evidence of $2ln(\text{BF})$ for those QTL locations with at least positive evidence, probability above 0.50, and support from visual inspection of trace plots and QTL intensity were calculated (Table 3). None of the identified QTLs showed strong evidence; however, QTLs on G5 and G6 were consistent across years, chromosomal positions, and traits.

The putative QTLs with an average positive evidence for FD were located on linkage groups G6 and G7 in 2011 and G5, G6, and G7 in 2012 (Table 3). Thus, the chromosomal locations with average positive evidence for FD observed across years were localized on linkage groups G5, G6, and G7, with the high effect of the QTL located on G5 in 2012. The QTLs on G5 and G7 had the highest average proportion of dominance genetic effects (0.004), followed by G6 (0.003), yet the contribution of the dominance genetic effects was low in proportion to the total σ_P^2 (Table 3).

Putative QTLs that exhibited an average positive evidence for FW were identified on G2 and G6, in 2011 and G5, G6, and G7 in 2012 (Table 3). Therefore, on average, QTLs located on G2, G5, and G6 showed positive evidence across years since G7 exhibited almost no evidence ($2ln(\text{BF}) = 0.40$) in 2011. The QTLs on G2, G5, and G6 showed dominance genetic effects; however, the values were infinitesimal (0.002, 0.005, and 0.001, respectively) with respect to the magnitude of σ_P^2, since the QTL on G2 exhibited the highest average proportion of σ_D^2 (0.008) for the entire study. Thus, the trait explaining the highest proportion of σ_P^2 by σ_D^2 was FW in 2012, with 1.3 %; however, the trait with the highest biannual proportion of σ_P^2 by σ_D^2 was FD with 1.1 % (Table 3).

The average proportion of σ_P^2 explained by additive genetic effects (σ_A^2) for QTL regions, with the exception of the region on G2 for the biannual exhibition of FW, was above 5 % (Table 3). Thus, for FD, approximately 13 % of σ_P^2 was explained by σ_A^2 of QTLs on G6 and G7 in 2011, approximately

Table 1 Values for phenotypic variance (σ_P^2), residual variance (σ_e^2), genetic variance (σ_G^2), additive genetic variance (σ_A^2), dominance genetic variance (σ_D^2), broad-sense heritability (H^2), and narrow-sense heritability (h^2) across years 2011 and 2012

Year	Trait	Records	μ_P	σ_P^2	Prior N_{QTL}	σ_e^2	σ_G^2	σ_A^2	σ_D^2	H^2	h^2	Linkage Group	2*ln*(BF)
2011	FD	264	64.09	175.881	1	0.17	0.26	0.08	0.83	0.83	0.26	G1	2.03
												G2	3.80
												G4	2.57
												G5	2.43
												G6	4.43
												G7	3.80
												G8	3.00
					3	0.18	0.10	0.01	0.82	0.83	0.10	G4	2.00
												G6	2.83
					5	0.17	0.10	0.00	0.83	0.83	0.10	G6	2.07
	FW	295	130.39	4220.85	1	0.21	0.22	0.01	0.79	0.79	0.22	G2	4.83
												G5	2.80
												G6	4.53
												G8	2.47
					3	0.21	0.10	0.10	0.79	0.79	0.10	G2	3.30
												G6	3.57
					5	0.22	0.12	0.00	0.78	0.78	0.12	G2	2.43
												G6	3.07
2012	FD	265	60.69	76.917	1	0.34	0.58	0.00	0.66	0.66	0.58	G1	2.27
												G4	2.07
												G5	5.33
												G6	3.10
												G7	5.50
												G8	2.17
					3	0.38	0.24	0.00	0.62	0.62	0.24	G5	3.70
												G7	2.83
					5	0.38	0.24	0.00	0.62	0.62	0.24	G5	2.87
												G7	2.07
	FW	286	119.40	2257.51	1	0.32	0.34	0.03	0.68	0.68	0.34	G1	2.17
												G2	2.07
												G3	2.43
												G4	2.20
												G5	5.70
												G6	4.13
												G7	5.17
					3	0.35	0.19	0.01	0.65	0.65	0.19	G5	3.17
												G6	2.73
												G7	2.73
					5	0.36	0.23	0.01	0.64	0.64	0.23	G5	2.70
												G6	2.83
												G7	2.23

Different values (1, 3, and 5) as priors for the number of QTLs (N_{QTL}), and Bayes Factors and chromosome locations of those QTLs with positive evidence for the exhibition of fresh fruit weight (FW) and fruit equatorial diameter (FD). Phenotypic mean and number of records per year are also shown

41 % by σ_A^2 of QTLs on G5, G6, and G7 in 2012, and for both years, the proportion of σ_P^2 explained by σ_A^2 was approximately 28 %, accounting for QTLs on G5, G6, and G7. Considering FW, the average amount of σ_P^2 explained by σ_A^2 was approximately 12 % from QTLs on G2 and G6 in 2011; approximately 23 % was explained by σ_A^2 from QTLs on G5,

Table 2 Average values for residual variance (σ_e^2), additive genetic variance (σ_A^2), dominance genetic variance (σ_D^2), genetic variance (σ_G^2), broad-sense heritability (H^2), and narrow sense heritability (h^2) for fresh fruit weight (FW) and fruit equatorial diameter (FD) per year and for the 2 years of study

Trait	σ_e^2	σ_A^2	σ_D^2	σ_G^2	H^2	h^2
Biannual FD	*0.27*	*0.25*	*0.02*	*0.73*	*0.73*	*0.25*
FD in 2011	0.17	0.15	0.03	0.83	0.83	0.15
FD in 2012	0.37	0.35	0.00	0.63	0.63	0.35
Biannual FW	*0.28*	*0.20*	*0.03*	*0.72*	*0.72*	*0.20*
FW in 2011	0.21	0.15	0.04	0.79	0.79	0.15
FW in 2012	0.35	0.25	0.01	0.65	0.66	0.25

G6, and G7 in 2012; and for both years, σ_A^2 explained approximately 16 % of σ_P^2 accounting for QTLs on G2, G6, and G7 (Table 3). A summary of the posterior positions of the QTLs per trait per year and the posterior additive and dominance genetic effects along linkage groups with positive evidence is shown in Fig. 4.

The region located on G5 between 3.66 and 8.70 Mb exhibited positive evidence for influence on both FD and FW, since the QTLs overlapped. Also, two contiguous QTLs between 14.89 and 22.35 Mb on G6 showed positive evidence for a joint influence on both traits. These results are consistent with the calculation of genetic correlation (ρ_G) of both traits, which was 0.82 in 2011 and 0.79 in 2012.

Table 3 Chromosomal location according to the assembly version 1.0 of peach (Verde et al. 2013) for putative QTLs and average evidence values by traits and years

Trait and year(s)	Linkage Group	Flanking markers	Location	Genetic Position (cM)	Average 2*ln*(BF)	$h^2_{A_{QTL}}$	$h^2_{D_{QTL}}$
FD in 2011	G6	ss_616119 ss_620099	03,792,224 04,809,346	14.89 16.95	3.11	0.073	0.004
	G7	ss_741710 ss_752524	06,657,446 08,336,521	21.46 27.86	2.22	0.053	0.007
FW in 2011	G2	ss_219973 ss_244929	07,508,139 11,310,097	14.81 16.92	3.52	0.050	0.002
	G6	ss_624248 ss_633314	06,337,567 09,264,750	19.20 22.35	3.72	0.069	0.001
FD in 2012	G5	ss_553912 ss_556209	02,580,963 03,212,441	5.12 7.08	3.97	0.155	0.000
	G6	ss_618417 ss_624248	04,320,514 06,337,567	16.03 19.20	2.00	0.104	0.002
	G7	ss_745637 ss_756641	07,350,828 09,508,457	24.24 31.54	3.47	0.148	0.001
FW in 2012	G5	ss_551012 ss_559057	02,085,084 03,731,230	3.66 8.70	3.86	0.082	0.008
	G6	ss_621195 ss_625354	05,163,919 06,801,914	17.95 19.75	3.23	0.075	0.000
	G7	ss_743631 ss_746629	06,943,483 07,471,270	22.63 24.71	3.38	0.075	0.005
Avg. FD over 2 years	G5	ss_553912 ss_556209	02,580,963 03,212,441	5.12 7.08	2.73	0.092	0.004
	G6	ss_616119 ss_624248	03,792,224 06,337,567	14.89 19.20	2.56	0.089	0.003
	G7	ss_741710 ss_756641	06,657,446 09,508,457	21.46 31.54	2.84	0.101	0.004
Avg. FW over 2 years	G2	ss_219973 ss_244929	07,508,139 11,310,097	14.81 16.92	2.49	0.032	0.002
	G5	ss_551012 ss_559057	02,085,084 03,731,230	3.66 8.70	2.71	0.059	0.005
	G6	ss_621195 ss_633314	05,163,919 09,264,750	17.95 22.35	3.48	0.072	0.001

The average evidence was calculated across genetic models with different priors and replications. Flanking markers are shown with their location and haplotypes coupling with the minor allele of the QTL (q), to avoid small fruits. Proportion of the phenotypic variance explained by additive $\left(h^2_{A_{QTL}}\right)$ and dominance $\left(h^2_{D_{QTL}}\right)$ genetic effects is also presented per QTL

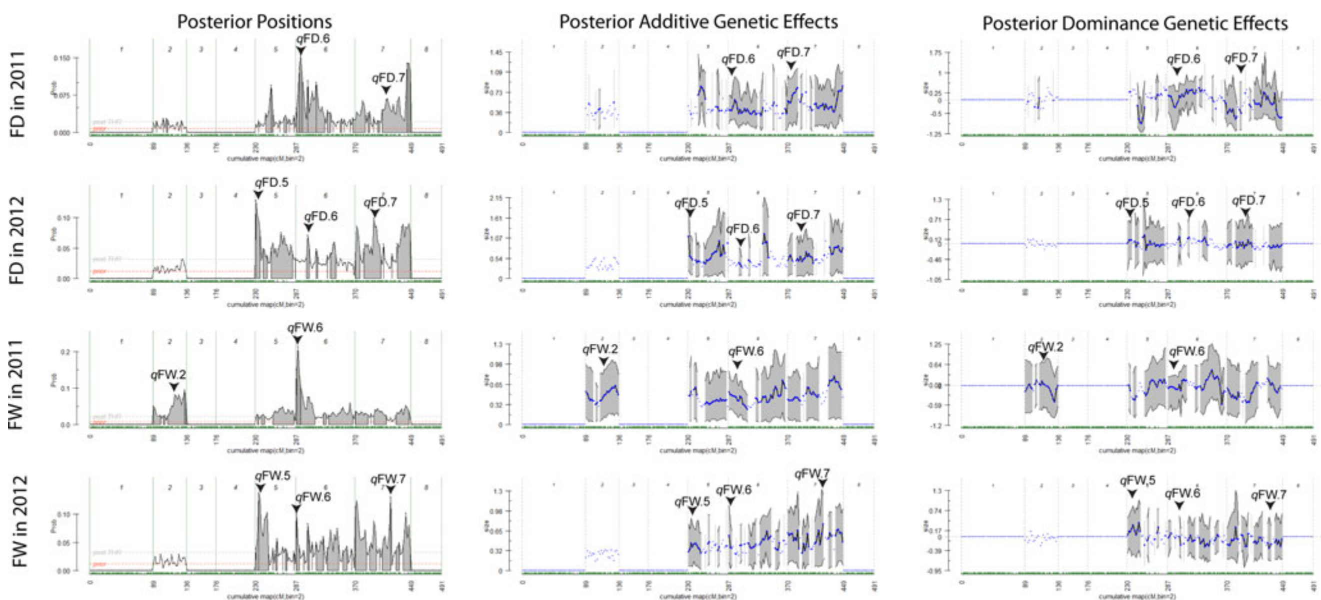

Fig. 4 Posterior chromosomal locations for QTLs with at least positive evidence for each trait in each year along with probabilities for the locations of posterior additive and dominance genetic effects. The *blue dots* represent the posterior mean and the *gray shade* the 90 % credible region for estimates of additive and dominance QTL effects.

Genomic breeding values

For all the individuals in the pedigree, genomic breeding values (GBVs) were estimated per trait per year (Online Resource 3) considering the genomic regions shown in Table 3. GBVs were highly correlated with the observed phenotypic values for all traits per year, suggesting high accuracy. In 2011, both FD and FW exhibited an accuracy of 0.93 each. In 2012, FD exhibited an accuracy of 0.87 and FW an accuracy of 0.89. The accuracy for both traits decreased in 2012, although the correlation among GBVs was significantly positive between years, at 0.45 and 0.46 for FW and FD, respectively. The general statistics for the GBVs obtained for this particular pedigree are presented in Table 4. The quantiles for GBVs are presented since they are of immediate relevance and used by breeders to decide the selection (in this case positive) intensity per trait. In Table 5, the genotypes for SNPs within a 1.65 Mb region falling into the interval of *q*FSz.5 and the GBVs for that region are shown for individuals of six progenies of the four breeding programs.

Table 4 Maximum, minimum, average, and quantiles for selection intensity of the genomic breeding values obtained for the pedigree studied

Trait	Year	Maximum	Minimum	Average	Quantiles		
					97.5 %	95 %	90 %
FD	2011	6.64	−7.30	1.39	5.36	5.06	4.62
	2012	15.14	−14.21	4.70	12.19	11.72	10.88
FW	2011	54.38	−53.47	−6.94	45.69	33.73	23.67
	2012	28.36	−27.55	0.28	17.05	14.05	11.86

Discussion

In this study, the genetic components influencing FD and FW were characterized using pedigree-based analysis (PBA) under the Bayesian framework. The pedigree analyzed included broad germplasm from the peach breeding programs of Clemson University, University of Arkansas, University of California at Davis, and Texas A&M University, with a common founder in the historical cultivar Orange Cling. The findings are supported by previous studies in peach and related *Prunus* species, primarily from QTL mapping, with the purpose of applying a breeding perspective to the genetic parameters ($\sigma^2_G, \sigma^2_A, \sigma^2_D,$ and ρ_G) and estimated GBVs. The methods used in this study illustrate an alternative strategy, geared toward geneticists and breeders working in active breeding programs, for the study of complex traits (e.g., flowering time, fruit quality and (a) biotic stresses). In the following sections, a discussion about the implications and support of each of the results yielded in this study is provided.

Pedigree

The pedigree used in this study is unique as its lineages are derived from heirloom cultivars that are founders of modern cultivars. Of the few studies which considered pedigree-connected segregating bi-parental populations of peach (de Souza et al. 1998a, b, 2000), our approach involved the identification of a subset pedigree based on common cultivar founders, followed by pedigree shrinkage for peach germplasm analyzed in the RosBREED project. Pedigree shrinkage was deployed in our study because four distinct breeding programs

Table 5 Genotypes for the SNP markers within the 1.65 Mb interval of *q*FSz.5 and 2-year average genomic breeding values (GBVs) for fruit equatorial diameter (FD) and fresh fruit weight (FW) for individuals and their parents represented in the pedigree studied here and from the four breeding programs (version in black and white available in Online Resource 4)

Name	Parent 1	Parent 2	ss_551012 2,085,084	ss_553912 2,580,963	ss_556209 3,212,441	ss_556975 3,427,608	ss_556982 3,427,826	ss_559057 3,731,230	FD[¶] 2-Year	FW[§] 2-Year
Goodwin	*DrDavis*	*11_11_37*	*AC*	*AG*	*AA*	*AA*	*AA*	*CC*	0.17	0.08
Vilmos	F8_72_33	F_F10C_12_28	*AC*	*AA*	*AG*	*AC*	*AG*	*AA*	-0.28	-0.13
CA_Pop_5_17_109	Goodwin	Vilmos	AC	AG	AG	AC	AG	AC	-0.21	-0.18
CA_Pop_5_17_047	Goodwin	Vilmos	AC	AG	AG	AC	AG	AC	-0.21	-0.17
CA_Pop_5_17_088	Goodwin	Vilmos	AC	AG	AG	AC	AG	AC	-0.21	-0.18
CA_Pop_5_17_093	Goodwin	Vilmos	AC	AG	AG	AC	AG	AC	-0.21	-0.18
CA_Pop_5_17_081	Goodwin	Vilmos	AC	AG	AG	AC	AG	AC	-0.18	-0.17
TX2B136	*Hermosillo*	*TXW1293_1*	*CC*	*AA*	*AG*	*AC*	*AG*	*CC*	-0.09	0.01
CAF4	*Y140_77*	*Y142_194*	*CC*	*AA*	*AA*	*AA*	*AA*	*CC*	0.00	0.03
TX_Pop1_15	TX2B136	CAF4	CC	AA	AG	AC	AG	CC	-0.16	-0.04
TX_Pop1_37	TX2B136	CAF4	CC	AA	AG	AC	AG	CC	-0.12	-0.04
TX_Pop1_19	TX2B136	CAF4	CC	AA	AG	AC	AG	CC	-0.15	-0.03
TX_Pop1_11	TX2B136	CAF4	CC	AA	AA	AC	AG	CC	-0.15	-0.02
TX_Pop1_35	TX2B136	CAF4	CC	AA	AA	AC	AG	CC	-0.15	-0.01
OHenry	MerrillBon	F_OHenry	*CC*	*AA*	*AA*	*AA*	*AA*	*CC*	0.08	-0.01
Cascata1006	*C92_16*	*F_Cascata1006*	--	--	--	--	--	--	-0.05	-0.01
SC_Pop0817_036	OHenry	Cascata1006	AC	AA	AG	AC	AG	AC	-0.07	-0.03
SC_Pop0817_052	OHenry	Cascata1006	AC	AA	AA	AC	AG	CC	-0.07	-0.01
SC_Pop0817_015	OHenry	Cascata1006	AC	AG	AG	AC	AG	CC	-0.06	0.01
SC_Pop0817_095	OHenry	Cascata1006	CC	AG	AA	AC	AG	CC	-0.06	0.01
SC_Pop0817_056	OHenry	Cascata1006	CC	AG	AA	AC	AG	CC	-0.06	0.02
A_776	*A_699*	*A_663*	*AC*	*AA*	*AG*	*AC*	*AG*	*AC*	0.05	-0.02
A_783	*A_699*	*A_717*	*AC*	*AA*	*AA*	*AA*	*AA*	*CC*	0.05	0.01
AR_Pop0801_09	A_776	A_783	AC	AA	AG	AC	AG	AC	0.04	-0.08
AR_Pop0801_10	A_776	A_783	AC	AA	AG	AC	AG	AC	0.05	-0.08
AR_Pop0801_12	A_776	A_783	AC	AA	AG	AC	AG	AC	0.05	-0.07
AR_Pop0801_01	A_776	A_783	AC	AA	AG	AA	AA	CC	0.04	-0.01
AR_Pop0801_14	A_776	A_783	AC	AA	AG	AA	AA	CC	0.04	0.01
BY92P2710	*Flameprince*	*87P943*	--	--	--	--	--	--	0.02	0.07
Bolinha	-	-	*CC*	*AA*	*AA*	*AA*	*AA*	*AA*	0.02	0.04
SC_Pop0821_001	BY92P2710	Bolinha	CC	AA	AA	AA	AA	AC	-0.04	0.05
SC_Pop0821_005	BY92P2710	Bolinha	CC	AA	AA	AA	AA	AC	-0.03	0.04
SC_Pop0821_010	BY92P2710	Bolinha	CC	AA	AA	AA	AA	AC	-0.03	0.04
SC_Pop0821_013	BY92P2710	Bolinha	CC	AA	AA	AA	AA	AC	-0.01	0.04
SC_Pop0821_017	BY92P2710	Bolinha	CC	AA	AA	AA	AA	AC	-0.01	0.04
DrDavis	*D25_9E*	*G40_5E*	*AC*	*AG*	*AG*	*AA*	*AA*	*CC*	0.11	0.01
D62_193	*NJC83*	*Conserva485*	*CC*	*AG*	*AA*	*AA*	*AA*	*CC*	0.22	0.16
CA_Pop_5_10_245	DrDavis	D62_193	AC	AG	AG	AA	AA	CC	0.19	0.08
CA_Pop_5_10_247	DrDavis	D62_193	AC	AG	AG	AA	AA	CC	0.19	0.10
CA_Pop_5_10_253	DrDavis	D62_193	AC	AG	AA	AA	AA	CC	0.19	0.14
CA_Pop_5_10_244	DrDavis	D62_193	CC	AG	AA	AA	AA	CC	0.19	0.16
CA_Pop_5_10_139	DrDavis	D62_193	CC	AG	AA	AA	AA	CC	0.21	0.17

AR University of Arkansas, *CA* University of California at Davis, *SC* Clemson University and *TX* Texas A&M University

[a] Green-shaded cells represent individuals with small-size fruits, yellow-shaded cells represent individuals with medium size fruits, and red-shaded cells represent individuals with large size fruits

[b] Green-shaded cells represent individuals with light-weight fruits, yellow-shaded cells represent individuals with medium-weight fruits, and red-shaded cells represent individuals with heavy weight fruits

serving different markets and therefore with different breeding targets were considered. The programs at Clemson University, University of Arkansas, and Texas A&M University breed primarily for regionally adapted, fresh market cultivars that typically exhibit freestone adhesion and melting flesh (although all breeders are actively incorporating all flesh types in order to diversify the market with new products). In contrast, the breeding program at the University of California at Davis develops processing cultivars with clingstone adhesion and non-melting flesh.

The entire RosBREED peach pedigree contained many founders and breeding lines with missing genotypic and

phenotypic information, which broke the traceable relationships required for the identity by decent (IBD) approach pursued though PBA. Therefore, for successful deployment of the PBA approach to QTL discovery and mapping, identification of pedigrees based on a common founder and subsequent shrinkage was a valid and useful strategy to enable the study of genetic components in perennial crop breeding situations beyond the type addressed here, since optimizing the information obtained by pedigree analysis leads to the estimation of genetic parameters and mapping of QTLs of immediate relevance for the breeding program(s) (Bink et al. 2002, 2008, 2012, 2014; van de Weg et al. 2004). In addition, although some cultivars were shared by breeding programs, no phenotypic records for the traits studied were available in every location which reduced the ability to discriminate between environmental and genetic effects.

This approach serves as a model for the study of complex traits across relevant germplasm from multiple fruit breeding programs. However, further improvements can be made through the addition of related progenies, by increasing the number of progenies in the full sib families, by developing complete phenotypic and genotypic data for all available accessions, and by recording phenotypic data for shared cultivars and important breeding parents replicated in all involved breeding programs. The common founder Orange Cling as well as others such as "O'Henry" would make particularly promising regional standards, given their relevance to all breeding programs.

Genetic map

The genetic distances predicted herein are supported by previous studies (Cabrera et al. 2009; Howad et al. 2005; Zhebentyayeva et al. 2008). These genetic distances are not derived from the actual construction of a linkage map and, to date, no peach consensus linkage map for QTL mapping in pedigreed outcrossing populations has been generated. Although our genetic map (RC^1) does not provide supporting information on the recombination rate within the germplasm studied, map development was successfully completed by taking advantage of framework markers developed as part of the *Prunus* bin map (Cabrera et al. 2009; Howad et al. 2005; Zhebentyayeva et al. 2008) with emphasis on maintaining the cytological accuracy of the RC^1 linkage map, which ultimately coincided with the results of genetic-by-physical distances from the Verde et al. (2013). The RC^1 linkage map covers a genetic distance (491 cM) similar to that of the *Prunus* bin map (519 cM), with even greater marker density (0.55 vs. 0.92 cM). This map is composed of predicted genetic distances developed using the physical locations of SNP markers to estimate their genetic distances through equations based on physical and genetic positions on the *Prunus* bin map. Thus, it provides a useful alternative when an actual consensus linkage map is not yet available for a diverse pedigree. Therefore, for crops in which genetic resources such as framework and consensus genetic maps are available, the procedure presented provides an alternative to expand the genetic understanding of the crop and accelerate progress toward the use of molecular marker technologies in breeding. Furthermore, this approach is more robust than using a constant conversion factor, which may misrepresent the cytological characteristics of a chromosome (e.g., position of a QTL in relation to the possible location of the centromere; Knox and Ellis 2002).

In peach, chromosome 1 is sub-metacentric, with chromosomes 2 and 4–7 being metacentric and chromosomes 3 and 8 being acrocentric (Jelenkovic and Harrington 1972). While a perfect agreement with the chromosome physical map is difficult to assess, the genetic distances presented show acceptable agreement with the cytological characteristics. The shape described by the polynomial linear function of the predicted genetic distances (Figure S1) for G1 exhibits a sub-metacentric shape, with a short arm formed at the beginning of the curve before the first elbow. Similarly, the shape of the curve for G2, G5, G6, and G7 displays metacentric structures as reported for chromosomes 2, 5, 6, and 7. Tendency curves for G3 and G8 indicate very similar acrocentric structures to those reported for chromosomes 3 and 8. The G4 tendency curve is the only one showing a more acrocentric shape, rather than the metacentric shape reported for chromosome 4 (Jelenkovic and Harrington 1972). In general, the conclusion is that the prediction of the genetic distances fits with the current knowledge of the cytology and the distribution of the molecular markers along linkage groups, which is supported considering the characteristics of the high quality reference genome (Verde et al. 2013). Knowledge of the relative position of a given QTL on a chromosome and its position with respect to centromere and telomeres is a first indicator of the likelihood to break linkages for suspicious linkage drag (Pea et al. 2013). Taking into account that as close to the centromere a locus is the recombination rates tend to decline, while at the extreme of the telomeres, recombination spots tend to occur (Esch and Horn 2008). Thus, until a new generation of linkage mapping using resources such as the IPSC 9K SNP array (Verde et al. 2012b) is developed, the approach used herein to predict genetic distances shows considerable promise for identifying markers with good quality control (polymorphic, no segregation distortion, and no or low missing data).

Genetic structure

As previously shown (Fresnedo-Ramírez et al. 2015a), the genetic structure underlying the RosBREED peach germplasm clusters are influenced by stone-adhesion/flesh-texture characteristics, formerly reported using non-melting and melting flesh peach cultivars in collections of Chinese (Aranzana

et al. 2010) and North American/European (Li et al. 2013) germplasm. Although genetic structure is an implicit characteristic of diverse pedigrees (Calboli et al. 2008), we suggest clustering of genetic structure in the form of group membership as a nuisance variable in the genetic model evaluated through PBA, since this method can reduce the confounding effects when two individuals at a locus possess the same marker alleles (identical by state (IBS)), but do not possess the same ancestry (identical by descent (IBD)). The vector for genetic structure added to the genetic model acted as a descent indicator, as discussed by Fresnedo-Ramírez et al. (2015a), helped to prevent slow convergence of the MCMC, which translates in less computing time to make sound statistical inferences.

Mapped QTLs and genetic parameters

Modeling yield components is desirable for crop improvement as the dissection of critical components aids in identification of their genetic control. Fruit size is a complex trait determined by initial cycles of carpel cell division followed by subsequent cell expansion to generate a fleshy mesocarp (Olmstead et al. 2007). Thus, while fruit weight (FW) and fruit diameter (FD) relate within a genotype, they vary in comparisons among genotypes because of differences in endocarp sizes as well as differences in mesocarp cell density. The multiple QTLs identified in this study for both FD and FW, and the two different ways to characterize fruit size (fresh weight and length of equatorial diameter), suggest complex genetic control of the trait. Some genetic components were shared, which was evident in the overlapping of QTLs, while others appeared to be specific for either FD or FW, which suggests that although the traits are tightly correlated, there are distinct components which may influence different processes (i.e., cell division and cell elongation).

In regard to FD, three putative QTLs designated *q*FD.5, *q*FD.6, and *q*FD.7 exhibited positive, 2-year evidence for FD on linkage groups G4, G5, G6, and G7. However, among these putative QTLs, only *q*FD.6 and *q*FD.7 exhibited stable positive evidence in both years. While other studies also support the importance of *q*FD.6, its position here, although contiguous, changed from year to year and was located in the upper region of G6, not the lower region as previously reported (Quilot et al. 2004). In the dissection of FD and FW in an F_2 progeny, da Silva Linge et al. (2015) found that a QTL in G7 explains the majority of the phenotypic variation for fruit size traits. Also, as in our study, a QTL for fruit cheek diameter, which could be considered the same as equatorial FD, was mapped on G5 (*q*FD.5) for only 1 year of evaluation, although on average, it exhibited positive evidence across both years. This QTL showed positive evidence only in 2012 and was located in a region of G5 lower than that identified by Quilot et al. (2004), but in which a stable, 2-year QTL for fruit suture diameter was also mapped. To date, no reports of detection of a QTL for FD on chromosome 7, such as *q*FD.7 in this study, have been described for peach bi-parental populations. In our study, qFD.7 was a stable QTL across years and in a co-localized region; however, our results agree with those showing a similar region mapped in the UC Davis pedigree analyzed by Fresnedo-Ramírez et al. (2015a), which also agrees with mapped QTLs for length of nut and kernel in the closely related almond (Fernández i Martí et al. 2013).

Likewise, complex control of FW was identified; *q*FW.2, *q*FW.5, *q*FW.6, and *q*FW.7 were identified as QTLs influencing FW, of which *q*FW.6 was the only QTL exhibiting positive evidence in both years. On average, *q*FW.2 and *q*FW.5 also showed positive evidence. *q*FW.2 co-localized with cherry QTLs for FW (Rosyara et al. 2013; Zhang et al. 2010), where the former study used a bi-parental population and the latter a PBA approach. Evidence of a stable QTL on G6 of peach for FW was found by da Silva Linge et al. (2015). In addition, in their study, the QTL found in G7 explained between 12 and 19 % of the phenotypic variation of FW, and a QTL on G5 in our study was significant for the year 2011 only. Our results are also in agreement with the linkage group location of a QTL for nut weight (Fernández i Martí et al. 2013). Furthermore, a QTL for peach fruit mass was also identified at the distal end of G2 (Quilot et al. 2004). Quilot et al. (2004) also identified QTLs for fruit mass on G5 and G7 in the first year of evaluation, which co-localized to some extent (both are located in the upper region of their respective linkage groups) with *q*FW.5 and *q*FW.7, both also identified in only 1 year, although the average evidence of *q*FW.5 in our study was positive for both years.

One particularly interesting QTL was *q*FW.6, since it co-localized with QTLs mapped for cherry (Rosyara et al. 2013; Zhang et al. 2010) and peach (Etienne et al. 2002). Additional support of this intriguing locus comes from a protein homology search for cell number regulator (*CNR*) genes, first performed on the peach reference genome sequence for later localization in cherry (De Franceschi et al. 2013). The candidate gene, *PpCNR20*, may be involved in modulating cell proliferation in the carpel ovary and has been validated in various crop species including tomato, maize, eggplant, and peppers (Guo and Simmons 2011). Another candidate gene, *CNR12*, is an important genetic element influencing fruit size (De Franceschi et al. 2013); however, in our study, *q*FW.2 did not show positive evidence in both years, although the average evidence was positive across years. In a representative pedigree of the University of California at Davis breeding program, Fresnedo-Ramírez et al. (2015a) also identified *G2FW* as a major QTL influencing fruit fresh weight in germplasm developed through a strategy of genetic introgression from related species.

Two genetic components simultaneously influencing FD and FW appear to be *q*FD.5 and *q*FW.5. Since *q*FD.5 and *q*FW.5 are co-localized, their denomination as joint locus

*q*FSz.5 (FSz standing for fruit size) is supported. However, further studies on *q*FSz.5 are necessary, since it is located on G5, a linkage group which showed low marker density in this study due to low levels of polymorphism. This low polymorphism rate has been observed when genotypes resulting from interspecific crosses, or as in this case, with genomic background from related species in previous generations (Verde et al. 2013) are incorporated, ultimately causing many SNPs to be excluded during marker selection.

Further studies on *q*FSz.5 are appropriate since a linkage disequilibrium (LD) peak related to domestication/breeding processes was proximally identified with this QTL (see Fig. 1 of Verde et al. (2013)), which further highlights the relevance of this genetic locus in control on peach fruit size. It is evident that although a domestication signature has important implication on fruit size (and it is usually assumed that fruit size in peaches is a fixed trait), there is still considerable diversity to be characterized, and the PBA has particular value for assessing breeding selections from multiple breeding programs with different objectives and strategies. It suggests that although genetic improvement and breeding are primarily reductionist activities in terms of diversity, the need for extending the narrow genetic base has enabled breeders to generate breeding stocks with differential allelic architecture in fixed traits. For example, low mass genotypes of peach were possible through the introgression of genetic material from almond, as occurred for the progeny between "Goodwin" × "Vilmos," in which the male parent possesses ±25 % almond genome from the cultivar "Tardy-Nonpareil." The availability of these kinds of genotypes facilitates the contrasting of allelic architectures for a more accurate genetic dissection of the traits. It may be applicable for some other complex traits such as flowering and ripening dates because a wide range of phenotypic expression for these traits is available across breeding programs.

Likewise, *q*FD.6 and *q*FW.6 also appeared to simultaneously influence FD and FW, further suggesting that *q*FD.6 and *q*FW.6 are contiguous elements and therefore indicating either a possible pleiotropic effect or one combined QTL, thus suggesting the denomination of a joint locus *q*FSz.6. These findings are supported by similar conclusions for suture and cheek diameters, fruit mass, and stone mass (Quilot et al. 2004). These discoveries and the high values estimated for ρ_G (0.82 in 2011 and 0.79 in 2012) similarly support a tight relationship between FD and FW, yet the study of common genetic components for these yield components has been limited. Furthermore, pleiotropic influences of other traits on peach size, such as maturity time (Eduardo et al. 2011) and acidity content (Etienne et al. 2002), are also beginning to be elucidated.

Throughout this discussion, we have emphasized the relevance of *q*FW.2, *q*FSz.5, *q*FSz.6, and *q*FD.7 as genetic elements controlling FD and FW, since taken together, they explain ~23 % of the phenotypic variance (accounting for both σ^2_A and σ^2_D). Individually, *q*FSz.5 explained, on average, ~7.5 % of the phenotypic variance through additive effects and ~0.5 % through dominance effects. The additive genetic effects are of particular importance, since they are more useful for achieving breeding goals due to their relative ease of manipulation. The QTL *q*FD.7 explained ~10 % of the phenotypic variance for FD through additive effects with no dominance effects, while *q*FSz.6 explained ~9 and 7 % of the phenotypic variance through additive effects for FD and FW, respectively. Additional studies are needed for *q*FW.2, which explained ~2 % of the phenotypic variance, since its relevance is limited by positive evidence for only 1 year, although its average was positive in both years.

It has been shown, primarily from studies by Hansche (Hansche et al. 1972; Hansche 1986a, b, 1988; Hansche and Boynton 1986), that traits such as FD and FW are largely influenced by additive genetic effects. The estimated values for h^2 in Hansche et al. (1972) suggest that 26 % of the phenotypic variance for FD is explained by additive effects, Scorza and Sherman (1996) 50 % for FW, and Souza et al. (1998) ~32 % for fruit mass, 38 % for cheek diameter, and 31 % for suture diameter. These conclusions are partially supported by our results, since h^2 for FD was between 0.16 and 0.31 and between 0.23 and 0.26 for FW. Moreover, the dominance effects did not exceed 3 % for either trait, even though the H^2 for both traits was between 0.64 and 0.83. The introduction of dominance effects into our analysis helped achieve convergence for stationary results, within an acceptable error in the MCMC chains, faster than with a pure additive genetic model. Thus, when a pure additive model was fitted, the number of iterations required to achieve convergence using the three values of priors for N_{QTL} was around 2.5 million. In contrast, after introducing the dominance effects into the genetic model, convergence was achieved with as few as 500, 000 iterations and the estimates of σ^2_G, σ^2_A, σ^2_D and ρ_G were stable and consistently independent from both the prior distributions applied for N_{QTL} and the starting values. We consider that the quicker convergence and stability of the results is a matter of re-distribution of the genetic variance between additive and dominance, which may imply an increase in the flexibility of the genetic model evaluated as more components are included.

These findings suggest that intra-allelic and inter-allelic interactions may play important roles in genetic control of these traits, as seen in pines (Hallander and Waldmann 2009; Waldmann et al. 2008), despite the small individual contribution of non-genetic effects for breeding purposes.

Because peach is propagated as a genetic clone, the directly assisted accumulation of additive genetic effects with synergistic, non-additive genetic effects is needed for optimal genetic improvement, trait consolidation, and cultivar development. Hallander and Waldmann (2007) suggested that

the amount of additive genetic variance is influenced by the presence of higher-order gene interactions such as dominance and additive-by-additive epistatic effects, yet the mechanisms for interactions of polygenic-multi-locus complexes are still not well understood. Recognizing this uncertainty, approaches such as the one proposed here are desirable for the identification of the genetic components as well as the gene-gene interactions influencing complex traits in vast amounts of inter-program-related breeding germplasm. Any advances in the accurate identification, estimation, and quantification of genetic components influencing a series of complex traits will improve breeding efficiency.

Genomic breeding values

Breeders have successfully developed strategies to consolidate genetic components which interact synergistically for desirable traits such as fruit size. Today, it is almost impossible to find advanced breeding accessions possessing undesirable characteristics, since for commercial success such accessions need to be at least as good as already available cultivars (Gradziel 2012). The need to achieve further genetic gain at an accelerated rate, while consolidating those gains in improved cultivars, remains a formidable challenge.

Bink et al. (2014) showed that GBVs from PBA are more accurate than those from genomic best linear unbiased prediction (G-BLUP) because ≥0.57 % of full sib families exhibited segregation for the trait under study (fruit firmness). In addition, the authors suggested that the relative low accuracy of GBVs for some full sib families may be due to undetected QTLs and non-additive effects involved in trait expression. In our study, the accuracy per family per trait and year in the pedigree was as low as 0.13 for FW in 2011 in the O'Henry × "Cascata1006" progeny and 0.48 in the "TX2293_3" × "CAF3 progeny; however, in 2012, their accuracies were 0.87 and 0.74, respectively, which suggests that these differences may be due to environmental and cultural management variance effects. For FD, none of the populations showed accuracies lower than 0.5, except some progenies from the University of Arkansas, which could simply be due to several missing values.

The GBVs for accessions were consistent with breeders' expertise, since the cultivars and breeding selections used as parents to fix high FW and FD and high GBVs had been previously established. However, most progenies exhibited lower values than commercial cultivars, which for FW, may be due to the bias generated by the typically higher crop density used in clingstone peach cultivars as well as the fresh market preference for fruit with larger FD. Nevertheless, the application of these GBVs will help optimize the information generated from QTL mapping through PBA, and thus to assist in parent selection.

A desirable extension of GBV estimation through PBA would be the incorporation of dominance effects, as done in pines (Hallander and Waldmann 2009; Waldmann et al. 2008) and pigs (Nishio and Satoh 2014). This addition enabled these studies to yield a more stringent and accurate ranking of parental value for marker-assisted parent selection (MAPS) of traits moderately to highly influenced by dominance genetic effects and might be exploitable for specific combining ability (Wricke and Weber 1986).

The current generation of additional genotypic information of the parents and ancestors in pedigrees and the prediction of the QTL genotypes (QQ, Qq, qQ, and qq) will increase reliability. This will allow determination of the allelic composition of the Mendelian components of QTLs for complex traits and subsequently enhance crossing decisions through MAPS, facilitating the crossing design (DeStefano and Hoeschele 1992; Kinghorn 1987). The determination of the allelic composition in our study was possible, but it lacked statistical reliability due to the gaps of genotypic information between founders as well as early and late generations. As more genotypic information from breeding program parents (cultivars and selections) is incorporated into pedigreed databases, the accuracy and quality of the information generated through strategies such as PBA will become more relevant for the community of perennial tree fruit breeders.

Conclusions and future prospects

The results noted herein are promising and serve as a framework for further studies using this pedigree as well as other Rosaceae (and virtually any perennial woody crop) pedigree which spans across multiple breeding programs such as currently being pursued in RosBREED: *Combining Disease Resistance with Horticultural Quality in New Rosaceous Cultivars* (Iezzoni et al. 2015). The current findings can be extended by studying the gene composition and allelic architecture of the identified QTLs, since together, these QTLs on average account for up to ~29 % of the phenotypic variation for FD and up to ~17 % for FW when additive and dominance effects were taken into account. The experience gained by applying PBA through this study should lead to improved methods for its application in future studies. This study can thus serve as a model for the use of PBA under the Bayesian framework to study the genetic components of complex traits of economic relevance both in related peach germplasm as well as other diverse perennial woody crop systems, aiding in the detection of QTLs of immediate relevance for several breeding programs simultaneously when the pedigree-connected germplasm is used. Enhancements in phenotypic and genotypic data collection and analysis, alongside improved phenotyping protocols, reduced costs for genotyping platforms, and more efficient bioinformatic approaches, will further enhance PBA results. In summary, our approach to

studying FD and FW consisted of identification of pedigrees based on a common cultivar founder, subsequent pedigree shrinkage, prediction of genetic distances using the *Prunus* bin map as a framework, accounting for genetic structure in the pedigree, and application of PBA to map QTLs and estimate GBVs and genetic parameters for direct incorporation of MAB. As detailed in the discussion, this approach represents a promising model to study genetic components of other complex traits of economic relevance, such as those related to phenologic changes, fruit quality, and post-harvest handling. The subsequent development of more efficient DNA tests to evaluate the genetic merits of parents and progenies in peach breeding will become invaluable tools to aid in the development of superior cultivars to meet the industries' evolving needs.

Acknowledgments This study was funded by USDA's National Institute of Food and Agriculture— Specialty Crop Research Initiative project, "RosBREED: enabling marker-assisted breeding in Rosaceae" (2009-51181-05808).

Jonathan Fresnedo Ramírez (the lead author) was supported by a CONACYT-UCMEXUS (Mexican Council of Science and Technology and University of California Institute for Mexico and the United States) doctoral fellowship at University of California, Davis.

Special thanks are given to Palma Lower, writing specialist at UC Davis, for her valuable comments and corrections during early stages of redaction of the manuscript.

Compliance with ethical standards

Conflict of interest The authors declare that there are no conflicts of interest.

Authors' contributions JFR phenotyped the accessions from UC Davis, carried out the analysis, and led the drafting of the manuscript. KG provided initial marker analysis IPSC 9K peach SNP array. TJF, PJS, and ASR helped in the selection of markers; phenotyped the selections from Clemson University, University of Arkansas; and drafted the manuscript. NA and TPH phenotyped the selections from Texas A&M University. MCAMB and EVW provided support for implementation and performing of PBA as well as for the interpretation of the results. CHC provided support for phenotypic evaluation and analyses. DHB, JRC, KG, and TMG provided the genetic materials and helped draft the manuscript. TMG coordinated the study and elaborated on the manuscript. All authors read and approved the final and reviewed manuscript.

Data archiving statement The QTL data and genomic breeding values (GBVs) reported in this manuscript will be made publicly available through the Genome Database for Rosaceae (www.rosaceae.org).

References

Abascal E, García Lautre I, Landaluce MI (2006) Multiple factor analysis of mixed tables of metric and categorical data. In: Multiple Correspondence Analysis and Related Methods. Chapman & Hall/CRC Statistics in the Social and Behavioral Sciences. Chapman and Hall/CRC, pp 351–367. doi:10.1201/9781420011319.ch15

American Pomological Society, Ragan WH (1899) Revised catalogue of fruits recommended for cultivation in the various sections of the United States and the British provinces by the American pomological society. U.S. Dept. of agriculture. Division of Pomology. Bulletin ;no. 8, vol 63 p. Govt. print. off., Washington

Aranzana MJ, Abbassi EK, Howad W, Arus P (2010) Genetic variation, population structure and linkage disequilibrium in peach commercial varieties. BMC Genet 11:69. doi:10.1186/1471-2156-11-69

Bai XF, Wu B, Xing YZ (2012) Yield-related QTLs and their applications in rice genetic improvement. J Integr Plant Biol 54:300–311. doi:10.1111/J.1744-7909.2012.01117.X

Bink MCAM, Uimari P, Sillanpaa MJ, Janss LLG, Jansen RC (2002) Multiple QTL mapping in related plant populations via a pedigree-analysis approach. Theor Appl Genet 104:751–762. doi:10.1007/s00122-001-0796-x

Bink MCAM, Boer MP, Braak CJF, Jansen J, Voorrips RE, de Weg WE (2008) Bayesian analysis of complex traits in pedigreed plant populations. Euphytica 161:85–96

Bink MCAM, Totir LR, ter Braak CJF, Winkler CR, Boer MP, Smith OS (2012) QTL linkage analysis of connected populations using ancestral marker and pedigree information. Theor Appl Genet 124:1097–1113. doi:10.1007/S00122-011-1772-8

Bink MCAM et al (2014) Bayesian QTL analyses using pedigreed families of an outcrossing species, with application to fruit firmness in apple. Theor Appl Genet 127:1073–1090. doi:10.1007/s00122-014-2281-3

Byrne DH, Bassols-Raseira M, Bassi D, Piagnani MC, Gasic K, Reighard GL, Moreno MA, Pérez S (2012) Peach. In: Badenes ML, Byrne DH (eds) Handbook of plant breeding, vol 5. Springer, New York, pp 505–569

Cabrera A, Kozik A, Howad W, Arus P, Iezzoni AF, van der Knaap E (2009) Development and bin mapping of a Rosaceae conserved ortholog set (COS) of markers. BMC Genomics 10 doi:Artn 562. doi:10.1186/1471-2164-10-562

Calboli FCF, Sampson J, Fretwell N, Balding DJ (2008) Population structure and inbreeding from pedigree analysis of purebred dogs. Genetics 179:593–601. doi:10.1534/Genetics.107.084954

da Silva Linge C, Bassi D, Bianco L, Pacheco I, Pirona R, Rossini L (2015) Genetic dissection of fruit weight and size in an F_2 peach (*Prunus persica* (L.) Batsch) progeny. Mol Breed 35:1–19. doi:10.1007/s11032-015-0271-z

De Franceschi P et al (2013) Cell number regulator genes in *Prunus* provide candidate genes for the control of fruit size in sweet and sour cherry. Mol Breed 32:311–326. doi:10.1007/S11032-013-9872-6

de Souza VAB, Byrne DH, Taylor JF (1998a) Heritability, genetic and phenotypic correlations, and predicted selection response of quantitative traits in peach: I. An analysis of several reproductive traits. J Am Soc Hortic Sci 123 (4):598–603

de Souza VAB, Byrne DH, Taylor JF (1998b) Heritability, genetic and phenotypic correlations, and predicted selection response of quantitative traits in peach: II. An analysis of several fruit traits. J Am Soc Hortic Sci 123 (4):604–611

de Souza VAB, Byrne DH, Taylor JF (2000) Predicted breeding values for nine plant and fruit characteristics of 28 peach genotypes. J Am Soc Hortic Sci Science 125 (4):460–465

DeStefano AL, Hoeschele I (1992) Utilization of dominance variance through mate allocation strategies. J Dairy Sci 75:1680–1690. doi:10.3168/jds.S0022-0302(92)77925-9

Eduardo I, Pacheco I, Chietera G, Bassi D, Pozzi C, Vecchietti A, Rossini L (2011) QTL analysis of fruit quality traits in two peach intraspecific populations and importance of maturity date pleiotropic effect. Tree Genet Genomes 7:323–335. doi:10.1007/S11295-010-0334-6

Esch E, Horn R (2008) Variability of recombination rates in higher plants. In: Lüttge U, Beyschlag W, Murata J (eds) Progress in botany, vol

69, Progress in botany. Springer, Berlin, pp 37–60. doi:10.1007/978-3-540-72954-9_2

Etienne C et al (2002) Candidate genes and QTLs for sugar and organic acid content in peach [*Prunus persica* (L.) Batsch]. Theor Appl Genet 105:145–159. doi:10.1007/S00122-001-0841-9

Fan S, Bielenberg DG, Zhebentyayeva TN, Reighard GL, Okie WR, Holland D, Abbott AG (2010) Mapping quantitative trait loci associated with chilling requirement, heat requirement and bloom date in peach (*Prunus persica*). New Phytol 185:917–930. doi:10.1111/J.1469-8137.2009.03119.X

Fanizza G, Lamaj F, Costantini L, Chaabane R, Grando MS (2005) QTL analysis for fruit yield components in table grapes (*Vitis vinifera*). Theor Appl Genet 111:658–664. doi:10.1007/S00122-005-2016-6

Fernández i Martí A, Font i Forcada C, Socias i Company R (2013) Genetic analysis for physical nut traits in almond. Tree Genet Genomes 9:455–465. doi:10.1007/S11295-012-0566-8

Font i Forcada C, Oraguzie N, Igartua E, Moreno MÁ, Gogorcena Y (2012) Population structure and marker–trait associations for pomological traits in peach and nectarine cultivars. Tree Genet Genomes 9:331–349. doi:10.1007/s11295-012-0553-0

Fresnedo-Ramírez J, Crisosto CH, Gradziel TM, Famula TR (2015a) Pedigree correction and estimation of breeding values for peach genetic improvement. Acta Hortic 1084:249–256. doi:10.17660/ActaHortic.2015.1084.35

Fresnedo-Ramírez J, Bink MCAM, van de Weg E, Famula TR, Crisosto CH, Frett TJ, Gasic K, Peace CP, Gradziel TM (2015b) QTL mapping of pomological traits in peach and related species breeding germplasm. Mol Breed 35(8):166. doi:10.1007/s11032-015-0357-7

Frett TJ, Gasic K, Clark JR, Byrne D, Gradziel T, Crisosto C (2012) Standardized phenotyping for fruit quality in peach [*Prunus persica* (L.) Batsch]. J Am Pomol Soc 66:214–219

Gradziel TM (2012) Traditional genetics and breeding. In: Kole C, Abbott AG (eds) Genetics, genomics and breeding of crop plants. CRC Press, Boca Raton, pp 22–54

Gradziel TM, Beres W, Pelletreau K (1993) Inbreeding in California canning clingstone peach cultivars. Fruit Varieties J 47:160–168

Guo M, Simmons CR (2011) Cell number counts—the fw2.2 and CNR genes and implications for controlling plant fruit and organ size. Plant Sci 181:1–7. doi:10.1016/J.Plantsci.2011.03.010

Hallander J, Waldmann P (2007) The effect of non-additive genetic interactions on selection in multi-locus genetic models. Heredity 98: 349–359. doi:10.1038/Sj.Hdy.6800946

Hallander J, Waldmann P (2009) Optimum contribution selection in large general tree breeding populations with an application to Scots pine. Theor Appl Genet 118:1133–1142. doi:10.1007/S00122-009-0968-7

Hansche PE (1986a) Heritability of juvenility in peach. HortScience 21: 1197–1198

Hansche PE (1986b) Heritability of fruit-quality traits in peach and nectarine breeding stocks dwarfed by the Dw gene. HortScience 21: 1193–1195

Hansche PE (1988) Two genes that induce brachytic dwarfism in peach. HortScience 23:604–606

Hansche PE, Boynton B (1986) Heritability of enzymatic browning in peaches. HortScience 21:1195–1197

Hansche PE, Beres V, Hesse CO (1972) Estimates of genetic and environmental effects on several traits in peach. J Am Soc Hortic Sci 97: 76

Hedrick UP, Howe GH, Taylor OM, Tubergen CB, New York State Agricultural Experiment Station., New York (U.S.: state). Department of Agriculture. (1917) The peaches of New York : report of the New York Agricultural Experiment Station for the year 1916. Annual Report / New York, U.S.: state, Department of Agriculture, vol 24 2 pt II. J.B. Lyon Co. printers, Albany

Howad W et al (2005) Mapping with a few plants: using selective mapping for microsatellite saturation of the *Prunus* reference map. Genetics 171:1305–1309. doi:10.1534/Genetics.105.043661

Iezzoni A (2010) RosBREED: enabling marker-assisted breeding in the Rosaceae. HortScience 45:S27–S28

Iezzoni A, Peace C, Bassil N, Coe M, Finn C, Gasic K, Luby JJ, Main D, McFerson J, Norelli J, Olmstead M, Whitaker VM, Chengyan Y (2015) RosBREED: Combining disease resistance with horticultural quality in new Rosaceous cultivars. XXIII Plant and Animal Genome Conference, San Diego 2015

Jannink JL, Bink MCAM, Jansen RC (2001) Using complex plant pedigrees to map valuable genes. Trends Plant Sci 6:337–342

Jelenkovic G, Harrington E (1972) Morphology of the pachytene chromosomes in Prunus persica. Can J Genet Cytol 14:317–324. doi:10.1139/g72-039

Jung S, Staton M, Lee T, Blenda A, Svancara R, Abbott A, Main D (2008) GDR (Genome Database for Rosaceae): integrated web-database for Rosaceae genomics and genetics data. Nucleic Acids Res 36:D1034–D1040. doi:10.1093/nar/gkm803

Jung S et al (2014) The Genome Database for Rosaceae (GDR): year 10 update. Nucleic Acids Res 42:D1237–D1244. doi:10.1093/nar/gkt1012

Kass RE, Raftery AE (1995) Bayes Factors. J Am Stat Assoc 90:773–795. doi:10.2307/2291091

Kinghorn B (1987) On computing strategies for mate allocation. J Anim Breed Genet 104:12–22. doi:10.1111/j.1439-0388.1987.tb00104.x

Knox MR, Ellis THN (2002) Excess heterozygosity contributes to genetic map expansion in pea recombinant inbred populations. Genetics 162:861–873

Lacape JM et al (2013) Mapping QTLs for traits related to phenology, morphology and yield components in an inter-specific *Gossypium hirsutum* x *G. barbadense* cotton RIL population. Field Crop Res 144:256–267. doi:10.1016/J.Fcr.2013.01.001

Le S, Josse J, Husson F (2008) FactoMineR: an R package for multivariate analysis. J Stat Softw 25:1–18

Li XW et al. (2013) Peach genetic resources: diversity, population structure and linkage disequilibrium. BMC Genet 14 doi:10.1186/1471-2156-14-84

Lippman Z, Tanksley SD (2001) Dissecting the genetic pathway to extreme fruit size in tomato using a cross between the small-fruited wild species *Lycopersicon pimpinellifolium* and *L. esculentum* var. giant heirloom. Genetics 158:413–422

Nishio M, Satoh M (2014) Including dominance effects in the genomic BLUP method for genomic evaluation. Plos One 9:e85792. doi:10.1371/journal.pone.0085792

Olmstead JW, Lezzoni AF, Whiting MD (2007) Genotypic differences in sweet cherry fruit size are primarily a function of cell number. J Am Soc Hortic Sci 132:697–703

Paterson AH, Lander ES, Hewitt JD, Peterson S, Lincoln SE, Tanksley SD (1988) Resolution of quantitative traits into Mendelian factors by using a complete linkage map of restriction fragment length polymorphisms. Nature 335:721–726. doi:10.1038/335721a0

Pea G, Aung HH, Frascaroli E, Landi P, Pe ME (2013) Extensive genomic characterization of a set of near-isogenic lines for heterotic QTL in maize (*Zea mays* L.). BMC Genomics 14:61

Peace CP, Crisosto CH, Gradziel TM (2005) Endopolygalacturonase: a candidate gene for freestone and melting flesh in peach. Mol Breed 16(1):21–31. doi:10.1007/s11032-005-0828-3

Peace CP, Luby JJ, van de Weg WE, Bink MCAM, Iezzoni AF (2014) A strategy for developing representative germplasm sets for systematic QTL validation, demonstrated for apple, peach, and sweet cherry. Tree Genet Genomes 10(6):1679–1694. doi:10.1007/s11295-014-0788-z

Peng B et al (2011) QTL analysis for yield components and kernel-related traits in maize across multi-environments. Theor Appl Genet 122: 1305–1320. doi:10.1007/S00122-011-1532-9

Portis E et al (2014) QTL mapping in eggplant reveals clusters of yield-related loci and orthology with the tomato genome. Plos One 9: e89499. doi:10.1371/journal.pone.0089499

Quarrie SA et al (2006) Dissecting a wheat QTL for yield present in a range of environments: from the QTL to candidate genes. J Exp Bot 57:2627–2637. doi:10.1093/Jxb/Erl026

Quilot B, Wu BH, Kervella J, Genard M, Foulongne M, Moreau K (2004) QTL analysis of quality traits in an advanced backcross between *Prunus persica* cultivars and the wild relative species P. davidiana. Theor Appl Genet 109:884–897. doi:10.1007/S00122-004-1703-Z

R Core Team (2013) R: a language and environment for statistical computing, 3.0.1 edn. R Foundation for Statistical Computing, Vienna, Austria

Rosyara UR et al (2013) Fruit size QTL identification and the prediction of parental QTL genotypes and breeding values in multiple pedigreed populations of sweet cherry. Mol Breed 32:875–887. doi:10.1007/S11032-013-9916-Y

Scorza R, Sherman BW (1996) Peaches. In: Janick J, Moore JN (eds) Fruit breeding. Wiley, New York, pp 325–440

Scorza R, Mehlenbacher SA, Lightner GW (1985) Inbreeding and coancestry of freestone peach cultivars of the eastern United States and implications for peach germplasm improvement. J Am Soc Hortic Sci 110:547–552

Semel Y et al (2006) Overdominant quantitative trait loci for yield and fitness in tomato. Proc Natl Acad Sci U S A 103:12981–12986. doi:10.1073/Pnas.0604635103

Shi J et al (2009) Unraveling the complex trait of crop yield with quantitative trait loci mapping in Brassica napus. Genetics 182:851–861. doi:10.1534/genetics.109.101642

Shulaev V et al (2008) Multiple models for Rosaceae genomics. Plant Physiol 147:985–1003. doi:10.1104/pp.107.115618

Sorensen D, Gianola D (2002) Likelihood, Bayesian and MCMC methods in quantitative genetics. Statistics for biology and health. Springer-Verlag, New York

Therneau T, Atkinson E, Sinnwell J, Schaid D, McDonnell S (2013) kinship2: Pedigree functions, 1.54 edn. http://CRAN.R-project.org/package=pedigree

van de Weg WE, Voorrips RE, Finkers R, Kodde LP, Jansen J, Bink MCAM (2004) Pedigree genotyping: a new approach of QTL identification and allele mining by exploiting breeding material. Acta Horticult 663:45–50

Venables WN, Ripley BD (2002) Modern applied statistics with S. Statistics and computing, 4th edn. Springer, New York

Verde I, Abbott AG, Scalabrin S, Jung S, Shu S, Marroni F, Zhebentyayeva T, Dettori MT, Grimwood J, Cattonaro F, Zuccolo A, Rossini L, Jenkins J, Vendramin E, Meisel LA, Decroocq V, Sosinski B, Prochnik S, Mitros T, Policriti A, Cipriani G, Dondini L, Ficklin S, Goodstein DM, Xuan P, Fabbro CD, Aramini V, Copetti D, Gonzalez S, Horner DS, Falchi R, Lucas S, Mica E, Maldonado J, Lazzari B, Bielenberg D, Pirona R, Miculan M, Barakat A, Testolin R, Stella A, Tartarini S, Tonutti P, Arus P, Orellana A, Wells C, Main D, Vizzotto G, Silva H, Salamini F, Schmutz J, Morgante M, Rokhsar DS (2013) The high-quality draft genome of peach (*Prunus persica*) identifies unique patterns of genetic diversity, domestication and genome evolution. Nat Genet 45: 487–U447. doi:10.1038/ng.2586

Verde I et al. (2012a) Development and Evaluation of a 9K SNP Array for Peach by Internationally Coordinated SNP Detection and Validation in Breeding Germplasm. Plos One 7 doi:ARTN e35668. doi:10.1371/journal.pone.0035668

Verde I, Gazza L, Aramini V, Taller DL, Dettori MT (2012b) A second generation peach linkage map using IPSC 9K SNP chip for advanced QTL identification. Paper presented at the RGC6 6th Rosaceous Genomics Conference, San Michele, Italy, June 2014 http://www.fruitbreedomics.com/index.php/the-results/posters/55-rgc6-6th-rosaceous-genomics-conference-2012-san-michele/77-verde-i-et-al-2012-a-second-generation-peach-linkage-map-using-the-ipsc-9k-chip-for-advanced-qtl-identification

Voorrips RE, Bink MCAM, van de Weg WE (2012) Pedimap: software for the visualization of genetic and phenotypic data in pedigrees. J Hered 103:903–907. doi:10.1093/Jhered/Ess060

Waldmann P, Hallander J, Hoti F, Sillanpaa MJ (2008) Efficient Markov chain Monte Carlo implementation of Bayesian analysis of additive and dominance genetic variances in noninbred pedigrees. Genetics 179:1101–1112. doi:10.1534/Genetics.107.084160

Wricke GN, Weber E (1986) Quantitative genetics and selection in plant breeding. W. de Gruyter, Berlin

Yamamoto T et al (2001) Characterization of morphological traits based on a genetic linkage map in peach. Breed Sci 51:271–278. doi:10.1270/jsbbs.51.271

Yu J, Buckler ES (2006) Genetic association mapping and genome organization of maize. Curr Opin Biotechnol 17:155–160. doi:10.1016/j.copbio.2006.02.003

Zdravkovic J, Zivoslav M, Mirjana M, Bogoljub Z, Milan Z (2000) Epistatic gene effects on the yield of the parents of F-1, F-2, BC1 and BC2 progeny. Acta Physiol Plant 22:261–265. doi:10.1007/S11738-000-0027-0

Zhang GR, Sebolt AM, Sooriyapathirana SS, Wang DC, Bink MCAM, Olmstead JW, Iezzoni AF (2010) Fruit size QTL analysis of an F_1 population derived from a cross between a domesticated sweet cherry cultivar and a wild forest sweet cherry. Tree Genet Genomes 6: 25–36. doi:10.1007/s11295-009-0225-x

Zhebentyayeva TN et al (2008) A framework physical map for peach, a model Rosaceae species. Tree Genet Genomes 4:745–756. doi:10.1007/S11295-008-0147-Z