HERITABILITY AND PHENOTYPIC CORRELATIONS IN PEACH

[Prunus persica (L.) Batsch]

A Thesis

by

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ABSTRACT

Fifteen peach [*Prunus persica* (L.) Batsch] horticultural and fruit quality traits were evaluated for two years at Fowler, CA and one year at College Station, TX to estimate heritability and phenotypic correlations. Seedlings from nine F_1 families along with parents used in crosses, were budded onto 'Nemaguard' rootstocks for evaluation. An all random effects model (REML) was used to estimate variance components and a multivariate model was used to estimate phenotypic correlations between traits.

High and moderate to high heritability was estimated for bloom date (h^2 = 0.62) and fruit ground color (h^2 = 0.50), while ripe date, fruit development period (FDP), fruit weight, red in the flesh, firmness, soluble solids, titratable acidity (TA), and pit weight showed low narrow sense heritability (h^2 = 0.05-0.24). These traits with low narrow sense heritability had moderate to high broad sense (H^2) heritability, indicating an important non-additive genetic component. Intermediate values of heritability (h^2 = 0.38 – 0.46) were found for pubescence, blush, fruit diameter, fruit tip, and fruit shape.

Two major genes had effects on additive heritability. Nectarine had a direct effect on heritability of fruit pubescence, while pantao shape and nectarine had pleiotropic effects on fruit diameter, resulting in higher estimates for both of these traits. Several traits (fruit red blush, fruit weight, fruit diameter, fruit tip, fruit shape, and fruit ground color, red in the flesh, fruit firmness, and soluble solids) were strongly affected by genotype by environmental interaction. Most traits exhibited substantial variability, which should allow for genetic improvement. Ripening date was strongly correlated (r =

0.94) with FDP, while bloom date was negatively correlated with FDP (r = -0.45) and fruit tip (r = -0.40). Ripening date and FDP were moderately correlated with fruit weight (r = 0.54, r = 0.50) and fruit diameter (r = 0.46, r = 0.45). Both measures of fruit size were strongly correlated (r = 0.77). Soluble solids was somewhat weakly correlated with ripening date and FDP (r = 0.32, r = 0.33). Pit weight was moderately correlated with FDP, fruit weight, and fruit diameter (r = 0.33, r = 0.51, r = 0.31, respectively).

DEDICATION

This thesis is dedicated to four special people who are responsible for who I am today:

Grandmother: Jeanne Newman Seale (1937-2007)

Grandfather: Hilmar Valentine Hartmann

Mother: Patricia Dianne Seale Hartmann

Father: Larry Hilmar Hartmann

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CHAPTER I

INTRODUCTION

Peach, *Prunus persica* (L.), is a small to medium deciduous fruit-bearing tree ranging from 4 to 10 meters in height in nature, although it is typically maintained at two to three for commercial production. It is a member of the sub-family Prunoideae in the Rosaceae family and is closely related to plum (*Prunus saliciana* (Lindl.) and *Prunus domestica* (L.)), apricot (*Prunus armeniaca* (L.)), and almond (*Prunus dulcis* (Mill.)) (Bassi and Monet, 2008). Cultivation of the fleshy fruit, which is classified as a drupe, was first reported over 3,000 years ago in its native China (Huang et al., 2008). Peach is a self-fertile fruit species that has been described as having low genetic variability, as compared to other crops, considering it is essentially derived from a single species (Scorza and Okie, 1990). Many of the fresh market peach cultivars developed in the United States in the 20th century are derived from a few accessions that were introduced into North America from Europe in the 18th century and a single introduction from China known as 'Chinese Cling' or 'Shanghai' (Scorza et al., 1985; Warburton and Bliss, 1996; Faust and Timon, 1995; Okie et al.,, 2008). The genetic variability of peach and nectarine is highest in its center of origin in China as compared to the rest of the world (Li et al., 2008; Yoon et al., 2006).

Development of new peach cultivars is possible by either outcrossing or inbreeding, as peach is self-compatible and tolerant of inbreeding. From a breeder's

perspective, peach does have several inherent disadvantages: relatively modest genetic variation compared to interspecific hybrid crops such as cotton, banana, and strawberry, and a long generation time compared to annual crops. Despite these challenges, peach is the most dynamic species among tree fruits with respect to the appearance of new cultivars in the market (Byrne, 2005; Fideghelli et al., 1998). Peach can be considered as a model genome because it is a diploid (2n=16) and has a small genome, which is approximately twice the size of the *Arabidopsis* genome (Abbott et al., 2002). Peaches are self-fertile, have little to no cross incompatibility either within or among related species, have relatively large flowers with accessible sexual organs, are precocious bearers compared to other perennial crops, and scion-types are clonally propagated.

Within the US, peach is the third most important tree fruit crop in terms of value ($723 million) and production with a total of 1,310,982 metric tons produced in 2010. World-wide, about twenty million metric tons of peaches are produced ranking fourth after grapes, apples, and pears in production (FAO STAT, 2010). The fruit are eaten fresh, but can also be frozen, canned, or dehydrated for storage and are processed for use in an array of products, ranging from confectionaries and flavorings to cosmetics.

The Texas A&M Stone Fruit Breeding Program focuses on both applied plant breeding and research studies related to the breeding and cultivation of the crop. The primary breeding target is the development of early-ripening, fresh market peaches and nectarines that require relatively low winter chilling. The ultimate goal of the applied program is the release of new commercial cultivars. The research part of the program focuses primarily on new technology and a better understanding of the crop's genetics

and diversity, which in turn is used to make the breeding program more efficient. Unfortunately, peach, like most fruit, often suffers from lack of quality and consistency. In fact, over past decade, peach and nectarine per capita consumption has been static, if not slightly decreased in the US (Anon., 2004). The most common consumer complaint for peaches was over the need for improved flavor and texture (Bruhn et al., 1991; Crisosto and Crisosto, 2005; Byrne, 2005). Recently, much of the focus for development of new peach and nectarine cultivars has been on better fruit quality, post-harvest quality, and novel traits (Byrne, 2005).

The objectives of this research were to determine:

1) Variance components of several horticultural and fruit quality traits including date of full bloom, date of ripening, fruit development period (FDP), fruit crop, fruit pubescence, fruit red blush, fruit weight, fruit diameter, fruit tip, fruit shape, split pits, fruit ground color, red in flesh, red around pit, fruit firmness, soluble solids, titratable acidity (TA) and pit weight.
2) Estimates of heritability in the narrow sense (h^2) and broad sense (H^2) for the above mentioned traits.
3) Genetic and phenotypic correlations among horticultural and fruit quality traits.

CHAPTER II

HERITABILITY AND PHENOTYPIC CORRELATIONS RELATING TO SEVERAL TREE AND FRUIT QUALITY TRAITS IN PEACH

2.1 Synopsis

Nine peach [*Prunus persica* (L.) Batsch] horticultural and fruit quality traits were evaluated for two years at Fowler, CA and one year at College Station, TX to estimate heritability and phenotypic correlations. Seedlings from nine F_1 families along with parents used in crosses were budded onto 'Nemaguard' rootstocks for evaluation. An all random effects model (REML) was used to estimate variance components and a multivariate model was used to estimate phenotypic correlations between traits. Bloom date was highly heritable (h^2 = 0.62), while ripening date, fruit development period (FDP), and fruit weight showed low narrow sense heritability (h^2 <0.20). These traits with low narrow sense heritability had moderate to high broad sense (H^2) heritability, indicating an important non additive genetic component. Intermediate values of heritability (h^2 = 0.38 – 0.46) were found for pubescence, blush, fruit diameter, fruit tip, and fruit shape. Two major genes had effects on additive heritability. Nectarine had a direct effect on heritability of fruit pubescence, while pantao shape and nectarine had pleiotropic effects on fruit diameter, resulting in higher estimates for both of these traits. Several traits (fruit red blush, fruit weight, fruit diameter, fruit tip, and fruit shape) were highly influenced by genotype by environment effects. All traits exhibited substantial

variability, which should allow for genetic improvement. Ripening date was strongly correlated (r = 0.94) with FDP, while bloom date was negatively correlated with FDP (r = -0.45) and fruit tip (r = -0.40). Ripening date and FDP were moderately correlated with fruit weight (r = 0.54, r = 0.50) and fruit diameter (r = 0.46, r = 0.45). Both measures of fruit size were strongly correlated (r = 0.77).

2.2 Introduction

The objectives of this research were to determine:

1) Variance components of several horticultural and fruit quality traits including date of full bloom, date of ripening, fruit development period (FDP), fruit crop yield, fruit pubescence, fruit red blush, fruit weight, fruit diameter, fruit tip, fruit shape, and split pits.

2) Estimates of heritability in the narrow sense (h^2) and broad sense (H^2) for the above mentioned traits.

3) Genetic and phenotypic correlations among horticultural and fruit quality traits.

2.2.1 Review of literature relating to horticultural and fruit quality traits in peach

Date of full bloom, typically recorded when 60% to 80% of flowers are open, is a reliable estimate of chilling (de Souza, 1996), and is controlled by both chilling requirement and heat unit accumulation (Rodriguez and Sherman, 1985). In peach, bloom time was reported to show a significant year effect (Cantin et al., 2009).

Heritability estimates range from moderate (h^2 = 0.39) (Hansche et al., 1972) to high (h^2 = 0.78; 0.90) (de Souza et al., 1998b; Monet and Bastard, 1982), suggesting qualitative gene action with potential for rapid genetic improvement (de Souza et al., 1998b). Phenotypically, bloom time was reported to have a weak negative correlation (r = -0.24) with fruit shape (Fruit length: average fruit diameter ratio), as fruit shape was found to be less desirable among later blooming genotypes. The genetic correlation was much stronger for these traits (r = -0.41) (de Souza et al., 1998b).

Date of ripening is affected by fruit crop load, cultural practices, weather conditions such as temperature, and genetics (Blake, 1930), and has been a focus of many breeding programs, particularly in the interest of developing earlier ripening varieties (Byrne, 2005). Estimates of heritability for date of ripening have ranged from high to very high (h^2 = 0.79 - 0.94) (Hansche., 1986; Hansche et al., 1972; de Souza et al., 1998b) supporting evidence of qualitative gene(s) as has been previously suggested (Hesse, 1975; Vileila-Morales et al., 1981). Date of ripening had a strong positive correlation with fruit development period (FDP) (r = 0.91), a moderately strong negative correlation with percent blush (r = -0.57), and moderately weak correlations with soluble solids (r = 0.41) and titratable acidity (r = 0.32) (de Souza et al., 1998b).

Fruit development period (FDP) has been defined as the interval between date of bloom and date of harvest (Blake, 1930), and like date of ripening, is influenced by both genetic and non-genetic factors (Weinberger, 1948). FDP appears to be more heavily influenced by date of ripening than date of bloom (Boonprakob et al., 1992; de Souza et al., 1998b; Weinberger, 1948) as earlier blooming does not necessarily result in a longer

development period. FDP was estimated to be highly heritable (h^2 = 0.73 - 0.98) (de Souza et al., 1998b; Monet and Bastard, 1982; Vileila-Morales et al., 1981). Fruit development period has a moderately weak correlation with titratable acidity (r = 0.37) and a strong correlation with the date of ripening (r = 0.91). The weak phenotypic correlation (r = 0.06) between FDP and fruit shape (length: average fruit diameter ratio) was much stronger as an estimate of only genetic correlation (r = -0.46). FDP was moderately correlated (r = 0.40) with soluble solids (de Souza et al., 1998b).

Fruit set is highly influenced by the environment, and environmental effects that can reduce fruit set include severe freezes during dormancy, late freezes during and following bloom, lack of chilling, warm winter temperatures, and high temperature and water stress during floral bud initiation. Ability for high fruit set following freeze events at or after the onset of bloom appears to be quantitatively inherited (Hesse, 1975), and is related to an adequate amount of flower bud survival resulting in high bud set in unfavorable environments (de Souza et al., 1998a). Yield is also highly influenced by the environment to which a crop is subjected, both during the fruiting season as well as the one prior (Jimenez and Diaz, 2002). Fruit set was estimated to have low to moderate heritability (h^2 = 0.09 - 0.53), suggesting possible potential for rapid genetic improvement (Perez, 1992; Rodriguez and Sherman, 1986; Jimenez and Diaz, 2002).

High percentage of red blush coverage on fruit surface is desirable for fresh market sale of peaches and nectarines in the U.S. (Beckman et al., 2005; Hesse, 1975), and is affected by temperature, exposure to light, and other environmental factors (Corelli-Grappadelli and Coston, 1991; de Souza, 1996). The amount of coverage and

intensity of red blush results from the expression of anthocyanins on the fruit skin (Layne et al., 2001) and has been evaluated either by using a subjective scale (Sherman et al., 1984) or based on the percent coverage of red on the fruit exterior (Byrne and Bacon, 1991). Red blush on peach has long been reported to be under polygenic control with heritability estimates ranging from moderate ($h^2 = 0.41$) to high ($h^2 = 0.68$) (Blake, 1932; Blake, 1940; Hansche, 1986; Weinberger, 1944; Hansche and Beres, 1980; de Souza et al., 1998b). Blush has shown a moderately strong negative correlation with time of ripening (r = -0.57) and fruit development period (r = -0.55), and a moderately weak negative correlation with soluble solids (r = -0.30) (de Souza et al., 1998b). In addition to these two recessive genes is a gene conditioning 100% blush (Beckman and Sherman, 2003), and another referred to as "high-lighter" that can suppress all red blush on fruit surface (Beckman et al., 2005). A major Quantitative Trait Loci (QTL) which explains 72% of the variation in blush has also been reported (Frett, 2012). Nectarines in some populations appear to have a higher percentage of red blush and darker shades of red than their peach siblings (Hesse, 1975; Wen, et al., 1995a; 1995b).

Fruit size is an important characteristic for the development of new varieties of peach and is influenced by environmental factors such as temperature as well as cultural practices including thinning and irrigation (Scorzal et al., 1991). Fruit size in fruits is a function of both cell number and cell size (Westwood et al., 1967), and can be measured as both fruit weight and fruit diameter (de Souza, 1996). Fruit size in peach appears to be quantitatively inherited, and has historically been believed to exhibit dominance for smaller size fruit (Hesse, 1975), although this has also been suggested to be an illusion

resulting from multiplicative action among traits controlling fruit size and mass (Hansche et al., 1972). Like sugar content, fruit size is highly influenced by many environmental factors (Marini and Sowers, 1994). Heritability for fruit size measured either by suture diameter or fruit mass has been estimated as being low (h^2 = 0.26 -0.29) to moderate (h^2 = 0.32 – 0.60), (Hansche and Beres, 1980; de Souza et al., 1998b; Hansche, 1986; Monet and Bastard, 1982; Hansche et al., 1972). Fruit size (suture diameter and fruit mass) is reported to be moderately correlated with fruit shape (r = 0.43 and 0.38 respectively) (de Souza et al., 1998b). Another study of segregating progeny found weak negative correlations for fruit mass and titratable acidity (r = -0.27) (Wu et al., 2003). Nectarine and pantao fruit consistently exhibited lower fruit size and mass compared to peach based on studies involving multiple crosses (Wang, 2009; Wu et al., 2003b) and another based on two peach cultivars and their respective nectarine mutants (Wen et at., 1995b).

Fruit shape is primarily a function of the prominence of the distil tip of the fruit as well as suture prominence. Fruit shape is influenced by chilling accumulation and temperature during fruit development, particularly during the early stages (de Souza et al., 1998b; Topp and Sherman, 1989b), and has traditionally been evaluated using a subjective scale (Rodriguez et al., 1986; Sherman et al., 1984; de Souza et al., 1998b). Fruit shape was estimated to be moderately heritable (h^2 = 0.43) (de Souza et al., 1998b). Genetically, fruit shape was reported to have a moderately strong correlation with fruit size (cheek diameter) (r = 0.49). (de Souza et al., 1998b). The “Pantao” fruit shape is conditioned by a single gene, showing complete dominance for saucer-shape fruit over

round fruit, although the genotypes homozygous for “Pantao” appears to be lethal (Hesse, 1975). Pantao fruits also appear to have higher soluble solids, but lower titratable acidity, flesh firmness, and weight based on segregating progeny (Wang, 2009).

2.2.2 Variance component and heritability

Overall peach fruit quality is a complex trait that is affected by genetics, the environment, environmental interaction with genetics, and cultural practices (Byrne, 2005; Crisosto et al., 1997). When selecting for superior cultivars, it is important to better understand all forces that contribute to the phenotype of the plant, as well as how they interact. Elementary Yield, fruit size, tree productivity, and other traits are reported to be under polygenic control. At present, many of these traits appear to have low heritability (Sansavini et al., 2006), which might be overcome by increasing variability through introgression of new material with greater relative variability for a particular trait.

An understanding of genetic parameters including variances, heritability, and relationships among traits can be very useful when attempting to make predictions of genetic progress over generations, particularly when selection of parents is based on their own performance (Falconer, 1989). One of the most important genetic concepts dealing with breeding is heritability, which partitions the genetic contribution to a plant’s phenotype from environmental effects. This will be a focus of this study.

Estimates of heritability can be used for predicting genetic progress for progeny when selection of parents is based on based on their own performance (de Souza et al., 1998a). Some traits appear to be highly heritable, so that they can be reliably and accurately measured, such that expression of such traits is not heavily influenced by differential interaction effects with the environment, while others have low heritability (Moing et al., 2003). Examples of highly heritable fruit quality traits in peach are: the percentage of skin red blush (h^2 = 0.68) (de Souza et al., 2000), the date of ripening (h^2=0.94) and fruit development period (FDP) (h^2 = 0.91) (de Souza et al., 1998b). Most studies on quantitative traits in peach have focused mainly on narrow-sense heritability (de Souza et al., 1998a) which considers only additive genetic variation and is most valuable to the breeder for making gains through selection. While these and other previously conducted studies have reported heritability and combining abilities in the case of tree fruit crops, most have consisted of progenies being evaluated on their own roots in the same location for multiple years.

Although earlier studies have arrived at heritability estimates by interpreting the genetic variance of a given progeny based on the covariance among relatives , recent studies have focused on estimating heritability on a progeny-mean basis expressed as the proportion of genetic (V_G or V_A) variance among a progeny to that of the phenotypic variance (V_P) (Bernardo, 2010). Linear regression of offspring performance on mid-parent performance has also been a useful method (Falconer, 1989), but is only an accurate estimate when the inbreeding coefficient is equal to zero (Fernandez and Miller, 1985). Although other methods of analysis based on variance components have been

used, most require robust experimental designs with reciprocal crossing and replications-all of which have limited feasibility in tree crops (de Souza, 1996).

Random effects models such as restricted maximum likelihood (REML) were developed and first used by animal geneticists (Searle, 1971; Henderson, 1983), and later by plant breeders (Vileila-Morales et al., 1981; McCutchan et al., 1985; Huber, 1994; Tancred et al., 1995). Studies by Vileila-Morales et al. (1981) and de Souza et al., (1998) have thus far been the only examples of using such a model for analyzing variance components in peach. In addition to providing generalized least squares estimation of fixed effects, providing flexibility in model specification for univariate and multivariate forms and correlated residual terms (Henderson, 1974; Huber, 1994), REML has critically proven to provide robust analysis with the use of unbalanced and non-normal data (Banks et al., 1985; Westfall, 1987).

2.2.3 Phenotypic correlations

Phenotypic correlation is determined from raw phenotypic values between two traits and accounts for both genetic and environmental correlations. Phenotypic correlations are mostly a function of environmental correlation when there is low heritability for a given trait (Falconer, 1989). Genetic correlations are primarily due to pleiotropy, but with low recombination, are also often the result of linkage. Genetic correlations are more useful when the heritability of the two measured traits is high (de Souza, 1996). Correlations between traits can be especially useful in plant breeding where indirect selection may be applied for a trait. For instance, selecting on a correlated

trait that is more easily measured than another highly correlated trait, assuming both traits have moderate to high heritability (Bernardo, 2010). Most correlations studies for peach and other fruit crops in the past have traditionally reported only on phenotypic correlations. It is important to keep in mind that the implication of phenotypic correlation in a breeding program is limited by the fact that both genetic and environmental correlations are included (de Souza et al., 1996). The same methods for estimating variance components such as mixed models can also be applied to calculate both phenotypic and genetic correlations, but parent-progeny models may also be used (Falconer, 1989). Typically, a bivariate analysis is used to compute correlations, and is carried out two traits at a time (Henderson, 1983).

2.3 Materials and methods

2.3.1 Plant material

Three hundred and ninety-six seedlings were randomly selected from nine F_1 families (Tables 1 and 2) created by crossing high sugar selections from the USDA Stone Fruit Breeding Program in Parlier, CA and medium to low chill selections from the Texas A&M University breeding program. The number of seedlings in each family ranged from 8 to 90. Parents used for crosses (Table 1) have shown to vary in the concentration of solids, ranging from 10.7 to 13.0 °Brix, and in chill requirement from approximately 150 to 650 chilling units. Other traits segregating in these progenies include fruit type (peach versus nectarine, round versus flat shape), fruit shape (prominence of tip and suture), fruit color (flesh and skin), fruit size, bloom date, ripe

Table 1. Parents and characteristics of peaches used in this study.

Genotype	Fruit type	Date of full bloom	Date of ripening	Fruit red blush	Fruit weight	Fruit diameter	Soluble solids	Titratable acidity	Notes
Y426-371	Ne-Yel	Feb 18	May 28	90	79.3	54.5	12.9	0.41	
Y434-40	Ne-Yel	Feb 6	May 16	70-90	75.6	54.5	12.7	0.44	
Y435-246	Ne-Yel	Feb 22	Jun 12	20-50	63.1	50.3	12.5	0.34	
Galaxy	Pc-Wh	Feb 19	Jun 12	40-70	140.9	76.9	12.6	0.24	Pantao[Y]
Victor	Pc-Yel	Feb 11	May 18	50-70	115.9	64.1	10.7	0.87	
TX2B136	Pc-Yel	Feb 5	Jun 2	60-80	119.8	63.4	11.0	1.29	
TX3E213LW	Pc-Wh	Feb 20	Jun 7	70-80	118.2	62.3	13.0	0.33	
TXW1490-1	Pc-Yel	Feb 5	Jun 8	30-40	107.6	61.9	12.2	1.0	

[Y]Pantao is heterozygous for round shape, homozygous pantao types do not survive

Date of full bloom and date of ripening expressed in days; fruit red blush visually based on % coverage of red blush on skin; fruit weight in grams; fruit diameter in millimeters; soluble solids in °Brix; titratable acidity in Eq H^+/1000 mL of juice

Table 2. Peach crosses and number of progeny evaluated.

Female		Male	Progeny
1	TX2B136	Y434-40	71
2	TX2B136	Y435-246	30
3	‘Victor’	Y426-371	90
4	‘Victor’	Y435-246	36
5	‘Victor’	‘Galaxy’	36
6	TX2B136	‘Galaxy’	50
7	TX3E213LW	Y434-40	50
8	TXW1490-1	Y434-40	25
9	TXW1490-1	Y435-246	8

date, productivity, and fruit development period.

Scion wood was collected from the parents and the original seedlings from breeding plots in College Station, TX and Floresville, TX. These were budded onto 'Nemaguard' peach rootstocks in the two evaluation plots in College Station, TX and Fowler, CA. Each site included one replicate of each seedling and three to four replicates of each parent.

2.3.2 Plot establishment and design

At the College Station site, one replicate of the propagated seedlings were randomized with four replicates of each parent in a randomized block design. At the Fowler site, plants were grouped according to progeny with the three to four replicates of each parent. In both cases, experimental blocks had border trees at the ends of each row and border rows immediately adjacent to the outer two rows. Parental genotypes were replicated to gain a better assessment of the phenotypic variance attributed to environmental effects.

Trees in the College Station plot were planted in staggered double-rows, with trees spaced 1.7 meters apart in double rows (0.67 meters apart). There were five meters between each group of double row (Figure 1). All trees were trained as a central leader.

Trees in the Fowler plot were trained as a two-scaffold 'Y' system and spaced

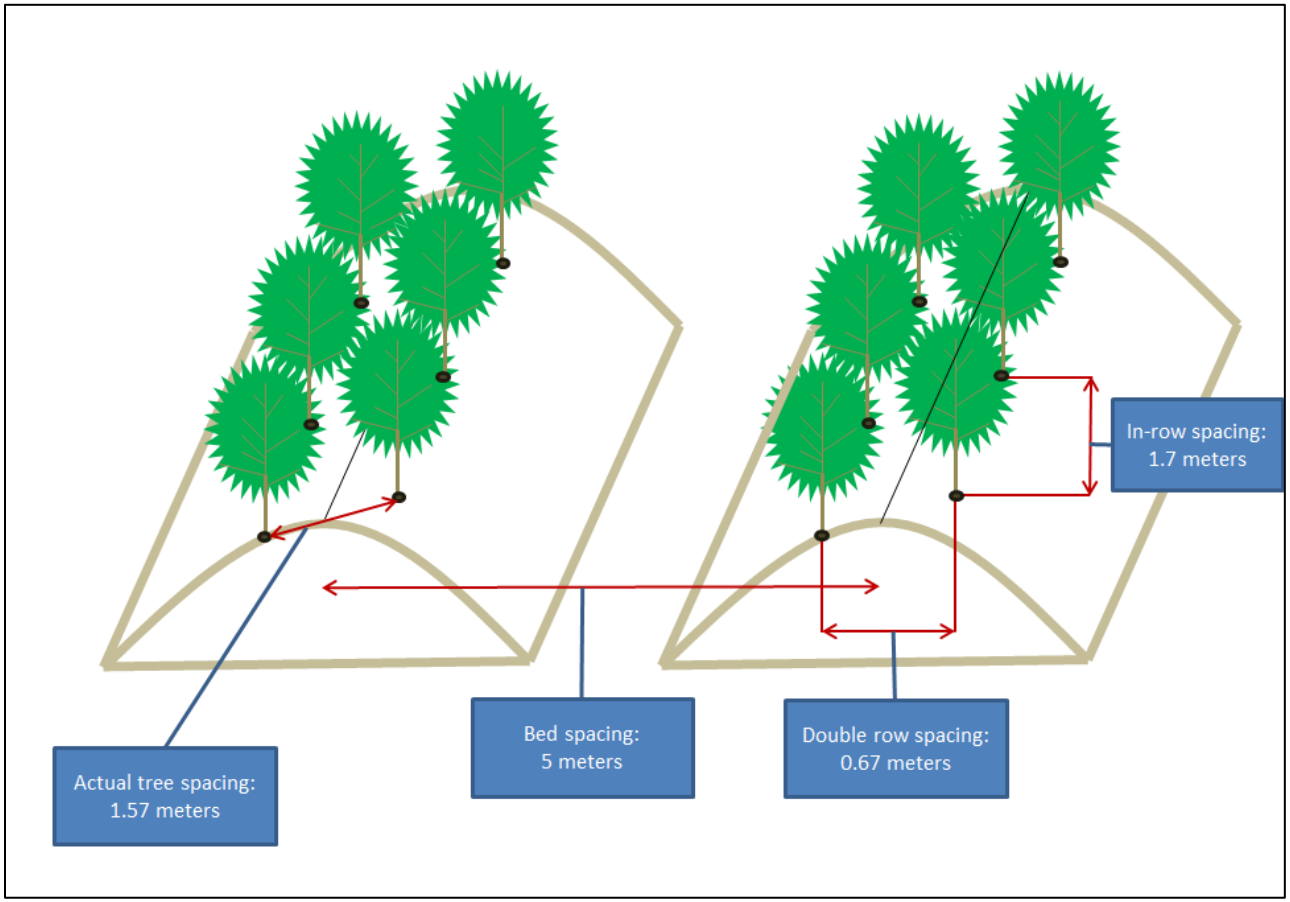

Figure 1. Planting scheme for College Station, TX site.

approximately one meter apart in single rows, approximately 4 meters apart. At each location, irrigation, fertilization, pest and weed control, pruning, and fruit thinning were carried out according to typical commercial practice.

Progenies and parents were evaluated at the two locations over two years (Table 3). Fowler, near Fresno, CA, is located in the center of the stone fruit producing San Joaquin Valley in central California and is ideal for peach production with a semi-arid Mediterranean climate. It has long, hot, dry summers and mild, wet winters. Fresno receives an average 284 mm rainfall per year, with temperatures ranging from 3.56°C (min. ave. Jan. temp) to 35.89°C (max. ave. July temp.). Fowler receives on average 80% of the total possible sunlight each year (Weather Underground, 2011). Situated in the middle of the Central Valley, the Fresno area has, for the most part, deep, alluvial sandy-loam soils with coarse texture and good internal drainage.

College Station is located in East Central Texas where stone fruit production in terms of acreage is comparatively small due to marginal soil and climate. The climate is described as sub-humid and warm temperate with mild winters and warm to hot, humid summers. College Station receives an average of 1000 mm rain per year, with temperatures ranging from 4.4°C (Min. Ave. Jan. Temp.) to 35.6°C (Max. Ave. July Temp.). College Station receives 27% less sunlight in a given year than does Fresno, except during the winter and early spring (Weather Underground, 2011). The College Station area is geographically nearly flat to slightly rolling hills, with the typical topsoil type a shallow moderately coarse sandy-loam to loamy sand with good internal drainage.

Table 3. A comparison of geography and climate between two sites.

	College Station, TX	Fresno, CA
Location	30°36'5" N, 96°18’52" W	36°44'52" N, 119°46'21" W
Average Elevation	112 m	90 m
Average Annual Rainfall	1000 mm	284 mm
Min. Ave. January Temperature	4.4°C	3.56°C
Max. Ave July Temperature	35.6°C	35.89°C
Ave. sunlight hours received	2578	3550
Climate	Sub-humid/warm temperate	Semi-arid/Mediterranean
Soil	Clay-pan	Alluvial sandy-loam

Data based on historical soil survey (USDA) and historical climate records (Weather Underground, 2011).

The region is also plagued with heavy clay subsoil with very poor structure and very limited internal drainage and aeration. The College Station site is plagued with poor quality water for irrigation, with high alkalinity and sodium levels. Compared to Fresno, College Station is much more likely to experience late damaging spring freezes, extreme temperature swings, and inconsistent rainfall (drought or flooding). Less and sporadic amounts of chilling received from year to year as well as warm temperatures during fruit development can also be major problems. The College Station site has higher humidity (favoring disease), warmer night temperatures, and lower sunlight during fruit development period: these collectively often result in relatively smaller fruit size, color, and soluble solids compared to the San Joaquin Valley. This overall makes College Station much less suitable for stone fruit production, which could allow it to be considered a stress environment.

2.3.3 Data collection

At both locations, data was recorded on 11 tree and peach fruit quality traits (Table 4). Data was collected for two years from the California plot (2011 and 2012) and one year from the Texas plot (2012) (Table 5). A severe drought and slow plant establishment resulted in no data being collected in Texas in 2011. Collection of data at the Texas site was conducted by the Texas A&M Stone Fruit Breeding Program. However, at the California site, the bloom data and fruit samples along with maturity data were collected by the staff of The Burchell Nursery where the block was planted. Pictures of each five fruit sample were taken of the exterior of the fruit from four

Table 4. Evaluation parameters of eleven peach tree and fruit quality traits.

Trait:	Parameter:	Units:
Date of full bloom	When 60-80% flowers open	Julian Days
Date of ripening	Determined by arrival of a few soft/edible fruit, remainder tree-ripe	Julian Days
Fruit development period (FDP)	Difference between date of full bloom and date of ripening	Days
Fruit crop	After normal thinning 0-9 scale	
Fruit pubescence	Scored using 0-9 scale	
Fruit red blush	Visually based on % coverage of red blush on skin using 0-5 scale	
Fruit weight	Average of five fruit	Grams
Fruit diameter	Across the cheek in mm, average of five fruit	Millimeters
Fruit tip	Visually assessed using 0-9 scale	
Fruit shape	Visually assessed using 0-9 scale (suture & tip)	
Split pits	Presence of fruit with pits split to the exterior (0-1)	

positions: top, cheek (one side), suture, and tip. Pictures were also taken by the Texas A&M Stone Fruit Breeding Program and Fruit Dynamics, Inc. following a combination of transverse and equatorial bisecting cuts revealing the interior of both remaining halves from each of the five cut fruit. Pictures were taken as possible of every entry at both locations.

2.3.4 Field evaluations

Full bloom date was visually assessed in the field and recorded when approximately 60% to 80% of the flowers had opened on each tree. Ripening date or maturity date was determined by the presence of a few fruit that were soft and able to be eaten off the tree, at which point a sample of five fruit were collected for further evaluation of other traits. Fruit were visually inspected in the field for maturity two times per week. Both full bloom date and maturity date were later converted to Julian days. Fruit development period (FDP) was calculated by subtracting the number of Julian days for full bloom date from that of maturity date.

Prior to harvest, a crop or productivity rating was assigned to each tree relative to typical commercial crop load. Because of the practice of normal fruit thinning, values lower than that of normal would suggest low flower set or abortion of young fruit. This information could also be used in contrast to fruit size, fruit diameter, and fruit soluble solids which have all reportedly been negatively correlated with crop load. The presence of split pits was originally measured by calculating the percentage of fruit with visible splitting based on a twenty fruit sample. This data was later converted to a binary scale

to simply indicate if a tree produced fruit in which splitting was observed.

2.3.5 Laboratory evaluations

Following harvest, the samples of five fruit were placed in plastic zip-lock bags at Fowler and paper bags at College Station, and placed in cold storage at 1°-4° C. for later evaluation. A five fruit sample was used for evaluation of all qualitative traits visually assessed. If expression for such traits was not uniform among all fruit in a given sample, an average or approximation was recorded. This evaluation took place either inside the TAMU Stone Fruit Breeding Lab or inside the Burchell Nursery building at Fowler under normal fluorescent lighting.

Fruit pubescence was visually evaluated on a 0-9 scale with 0 indicating an absence of fuzz and 9 as extremely fuzzy. Most modern commercial varieties were placed in the 3-5 range. Fruit red blush was characterized by the amount of red pigmentation on the outside of the fruit. Visual ratings were assigned based on observation of five fruit using the following scale: 0 = <1% blush, 1 = 1% to 20% blush, 2 = 21% to 50% blush, 3 = 51% to 80% blush, 4 = 81% to 99% blush, 5 = 100% blush.

Fruit tip was subjectively evaluated on a 0-9 scale based on the prominence of the tip at the distal end of the fruit in which a lower number rating would indicate a more prominent tip, while a higher number would indicate a less prominent or more oblate tip. Fruit shape was also subjectively evaluated using a 0-9 scale in which a higher number rating would indicate a more desirable fruit shape with a less prominent suture bulge and oblate tip.

Fruit mass (grams) is the average weight of a five fruit sample. Weight measurements from the Fowler location were taken by the staff at Fruit Dynamics lab (2665 N. Air Fresno Dr. Fresno, CA 93727). Fruit diameter was determined by measuring across the fruit cheek using a standard caliper based on the average of five fruit and was reported in millimeters.

2.3.6 Statistical analysis

All statistical analyses were performed using JMP software, Version 9.0, SAS Institute Inc., Cary, NC, 1989 – 2010.

Prior to statistical analyses, data were tested for normality using a Shapiro-Wilcox test. Data from all traits proved to be non-normally distributed. An array of transformations were performed and tested for normality, all of which resulted in the assumption of normality not being met. In addition to testing the effectiveness of each transformation with regard to normality, the model for variance components was also run using the data resulting from each transformation. Output from the analysis model (below) was compared to that of the non-transformed data by evaluating the R^2 value and the genotypic variance component value. In every case, these values were smaller than that of the non-transformed data. Therefore the non-transformed data were used throughout this study.

The additive genetic (σ^2_a), non-additive genetic (σ^2_{di}), environmental (σ^2_e), and genotype x environment (σ^2_{gxe}) variances were estimated using a restricted maximum likelihood (REML) mixed model with all random effects. The variances are reported

from the covariance parameter estimate report in JMP. There were three sets of data: Fowler, 2011; Fowler, 2012; College Station, 2012. Year 2012 was found to have differing effects in the CA and TX different locations, so year and location were treated as single environments including: CA-2011, CA-2012, and TX-2012. Parentage (male and female) was also taken into account for all progenies.

Because there was no replication included in the model (only the parents were replicated), there was no residual and all variance was partitioned into one of the following components: σ^2_a (additive genetic); σ^2_{di} (non-additive genetic); (σ^2_e) environmental; σ^2_{gxe} (genotype x environment).

Broad sense heritability estimates were calculated as:

$$H^2_{bi} = \frac{\hat{\sigma}^2_G}{\hat{\sigma}^2_G + \frac{\hat{\sigma}^2_{GE}}{e}}$$

Narrow sense heritability estimates were calculated as:

$$h^2_{bi} = \frac{\hat{\sigma}^2_A}{\hat{\sigma}^2_G + \frac{\hat{\sigma}^2_{GE}}{e}}$$

Where,

$\hat{\sigma}^2_A$ = estimated additive genetic variance

$\hat{\sigma}^2_G$ = estimated genetic variance

$\hat{\sigma}^2_{GE}$ = estimated genotype x environment variance

e = number of environments

A bivariate model was used to estimate phenotypic correlations. Correlations were computed on a pair-wise basis for all traits. Significance of correlation estimates were discussed based on the magnitude of the estimate because the sampling variances for the correlation estimates were not available (de Souza et al., 1998a). Thus, correlation estimate of ≥0.65 was considered strong to very strong; a correlation estimate between 0.50 and 0.64 was considered moderately strong; a correlation estimate between 0.30 and 0.49 were considered moderately weak.

Table 5. Number of observations used in variance component and heritability estimates for eleven peach tree and fruit quality traits evaluated for two years at Fowler, CA and for one year at College Station, TX.

Trait	Number of observations
Date of full bloom	726
Date of ripening	805
Fruit development period	715
Fruit crop	639
Fruit pubescence	721
Fruit red blush	715
Fruit weight	675
Fruit diameter	679
Fruit tip	711
Fruit shape	716
Split pits	502

2.4 Results and discussion

2.4.1 Variance component and heritability

A substantial amount of variability was associated with date of full bloom as indicated by the range (29 to 70 days) with a mean of 46.17 among progeny (Table 6). This was not unexpected as date of full bloom of parents used for crosses ranged from January 20 to March 1 (20 to 61 Julian Days) (Table 7) and by the fact that this trait is believed to be qualitative (de Souza et al., 1998b). Bloom, however appeared to have considerably less variability compared to date of ripening and fruit development period (FDP). Bloom date was strongly affected by the environment (Table 8), as trees bloomed approximately nine and seven days earlier on average at Fowler in 2011 and 2012, respectively, than at College Station in 2012 (Table 9). Although the average bloom date at College Station in 2012 was later than at Fowler for both years, both the range and standard deviation observed for this environment (Table 9) suggests that lack of chilling might have contributed to this difference. While low chill genotypes bloomed early, bloom of higher chill genotypes was delayed by insufficient chilling, which resulted in a higher mean bloom date at College Station in 2012. The College Station site received considerably less chilling in 2012 (530 chilling units) than did the Fowler site in 2011 and 2012 (909 and 978 chilling units respectively). Date of full bloom was found to highly heritable, due to a high level of additive inheritance ($h^2 = 0.62$ (Table 8).This was intermediate between estimates previously reported ($h^2 = 0.39, 0.78, 0.90$) (Hansche et al., 1972; de Souza et al., 1998b; Monet and Bastard, 1982). The appreciable genetic

Table 6. Descriptive statistics of nine peach tree and fruit quality traits evaluated for nine progeny for two years at Fowler, CA and one for year at College Station, TX.

Trait[w]	N	Mean	Phenotypic Variance	Standard Deviation	C.V.	Min	Max
Date of full bloom	726	46.2	52.72	6.88	14.90	29.0	70.0
Date of ripening	805	145.5	464.8	19.67	13.52	101.0	204.0
FDP	715	98.4	555.62	21.86	22.21	50.0	159.0
Fruit pubescence	721	3.5	3.43	1.82	52.30	0.0	7.0
Fruit red blush	715	3.0	0.69	0.77	25.93	1.0	5.0
Fruit weight	675	102.5	1201.96	32.06	31.27	12.0	250.0
Fruit diameter	679	58.4	58.08	6.63	11.36	36.3	87.6
Fruit tip	711	7.7	0.79	0.81	10.51	5.0	9.0
Fruit shape	716	7.3	0.57	0.71	9.75	5.0	9.0

N = Number of observations; C.V. = coefficient of variation; Min = minimum value; Max = maximum value.

[w]Date of full bloom and date of ripening expressed in Julian Days; FDP = fruit development in days; fruit pubescence visually based on 0-9 scale (0 = no pubescence, 6 or higher = greater pubescence than modern cultivars); fruit red blush visually based on % coverage of red blush on skin using 0-5 scale (0 = 0% red coverage, 1 = 1%-20%, 2 = 21%-50%, 3 = 51%-80%, 4 = 81%-99%, 5 = 100%); fruit weight in grams; fruit diameter in millimeters; fruit tip visually based on 0-9 scale (6 or lower = very prominent fruit tip, 9 = completely oblate fruit tip); fruit shape visually based on 0-9 scale (6 or lower = large suture bulge and prominent tip, 9 = no pronounced suture and oblate tip).

Table 7. Descriptive statistics of nine peach tree and fruit quality traits evaluated for eight parents for two years at Fowler, CA and one for year at College Station, TX.

Trait [w]	N	Mean	Phenotypic Variance	Standard Deviation	C.V.	Min	Max
Date of full bloom	55	45.3	76.56	8.75	19.33	20.0	61.0
Date of ripening	66	151.9	253.45	15.92	10.48	125.0	179.0
FDP	55	106.1	281.90	16.79	15.83	66.0	133.0
Fruit pubescence	64	2.5	4.20	2.05	81.35	0.0	6.0
Fruit red blush	64	3.0	0.53	0.73	24.58	1.5	5.0
Fruit weight	61	106.0	1090.98	33.03	31.17	43.0	175.0
Fruit diameter	60	62.3	90.06	9.49	15.24	47.4	87.7
Fruit tip	63	8.1	0.98	0.99	12.18	6.0	9.0
Fruit shape	63	7.5	0.69	0.83	11.01	6.0	9.0

N = Number of observations; C.V. = coefficient of variation; Min = minimum value; Max = maximum value.

[w]Date of full bloom and date of ripening expressed in Julian Days; FDP = fruit development in days; fruit pubescence visually based on 0-9 scale (0 = no pubescence, 6 or higher = greater pubescence than modern cultivars); fruit red blush visually based on % coverage of red blush on skin using 0-5 scale (0 = 0% red coverage, 1 = 1%-20%, 2 = 21%-50%, 3 = 51%-80%, 4 = 81%-99%, 5 = 100%); fruit weight in grams; fruit diameter in millimeters; fruit tip visually based on 0-9 scale (6 or lower = very prominent fruit tip, 9 = completely oblate fruit tip); fruit shape visually based on 0-9 scale (6 or lower = large suture bulge and prominent tip, 9 = no pronounced suture and oblate tip).

Table 8. Variance component, broad sense heritability (H^2), and narrow sense heritability (h^2) for nine peach tree and fruit quality traits evaluated for two years at Fowler, CA and for one year at College Station, TX.

Trait [w]	Variances[y]						H^2	h^2
	V_A	V_{DI}	V_G	V_E	V_{GxE}	V_P		
Date of full bloom	17.86	5.62	23.48	13.56	15.68	52.72	0.82	0.62
Date of ripening	17.24	222.11	239.35	158.91	66.55	464.8	0.92	0.07
FDP	17.11	227.75	244.36	239.74	71.02	555.62	0.91	0.06
Fruit pubescence	1.52	2.02	3.54	0.1	0.73	3.43	0.94	0.40
Fruit red blush	0.18	0.08	0.26	0.02	0.40	0.69	0.66	0.46
Fruit weight	96.59	358.62	455.21	217.95	528.81	1201.96	0.72	0.15
Fruit diameter	17.64	14.16	31.62	4.63	21.83	58.08	0.81	0.45
Fruit tip	0.18	0.13	0.31	0.12	0.36	0.79	0.72	0.42
Fruit shape	0.09	0.02	0.11	0.07	0.39	0.57	0.46	0.38

[y]V_A = additive genetic variance; V_{DI} = non-additive genetic variance; V_G = genetic variance (additive and non-additive); V_E = environmental variance; V_{GxE} = genotype x environmental variance; V_P = phenotypic variance

[w]Date of full bloom and date of ripening expressed in Julian Days; FDP = fruit development period in days; fruit pubescence visually based on 0-9 scale (0 = no pubescence, 6 or higher = greater pubescence than modern cultivars); fruit red blush visually ba
sed on % coverage of red blush on skin using 0-5 scale (0 = 0% red coverage, 1 = 1%-20%, 2 = 21%-50%, 3 = 51%-80%, 4 = 81%-99%, 5 = 100%); fruit weight in grams; fruit diameter in millimeters; fruit tip visually based on 0-9 scale (6 or lower = very prominent fruit tip, 9 = completely oblate fruit tip); fruit shape visually based on 0-9 scale (6 or lower = large suture bulge and prominent tip, 9 = no pronounced suture and oblate tip).

Table 9. Comparison of nine peach tree and fruit quality traits evaluated for nine progeny in three environments.

	Fowler, CA 2011		Fowler, CA 2012		College Station, TX 2012	
Trait [w]	Mean	Min-Max	Mean	Min/Max	Mean	Min/Max
Date of full bloom	42.4	36.0-59.0	44.2	36.0-51.0	51.4	29.0-70.0
Date of ripening	155.6	119.0-204.0	148.3	125.0-195.0	131.0	101.0-185.0
FDP	113.5	78.0-156.0	104.2	74.0-159.0	80.1	50.0-136.0
Fruit pubescence	3.6	0.0-7.0	3.5	0.0-7.0	3.2	0.0-6.0
Fruit red blush	3.1	2.0-5.0	2.8	1.00-5.00	3.1	2.0-4.5
Fruit weight	116.8	52.0-250.0	105.5	31.6-204.4	89.2	12.0-185.2
Fruit diameter	60.4	36.3-87.6	59.7	40.7-75.2	56.8	42.4-79.6
Fruit tip	8.0	6.0-9.0	7.7	6.0-9.0	7.2	5.0-9.0
Fruit shape	7.6	6.0-9.0	7.1	5.0-9.0	7.2	5.0-9.0

[w]Date of full bloom and date of ripening expressed in Julian Days; FDP = fruit development in days; fruit crop as relative to commercial crop based on 0-9 scale (0 = no crop, 5 = full crop, 6 or higher = excess crop); fruit pubescence visually based on 0-9 scale (0 = no pubescence, 6 or higher = greater pubescence than modern cultivars); fruit red blush visually based on % coverage of red blush on skin using 0-5 scale (0 = 0% red coverage, 1 = 1%-20%, 2 = 21%-50%, 3 = 51%-80%, 4 = 81%-99%, 5 = 100%); fruit weight in grams; fruit diameter in millimeters; fruit tip visually based on 0-9 scale (6 or lower = very prominent fruit tip, 9 = completely oblate fruit tip); fruit shape visually based on 0-9 scale (6 or lower = large suture bulge and prominent tip, 9 = no pronounced suture and oblate tip).

variability for this trait, along with its moderate heritability, should allow for genetic improvement.

A great deal of variability was observed for both date of ripening and FDP, as evidenced by the wide range (101 to 204 days) for ripening and (50 to 159) for FDP among progeny (Table 6). These ranges were closely aligned with, but higher than those of the parents for ripe and FDP (125 to 179 and 66 to 133, respectively) (Table 7). This, along with the observation of transgressive segregation suggests very high variability. Both of these traits were affected strongly by the environment (Table 8). Fruit, on average, ripened approximately 25 and 17 days later and had development periods that were approximately 34 and 24 days longer at Fowler in 2011 and 2012, respectively, than at College Station in 2012 (Table 9). This was likely an effect of cooler temperatures during the months of fruit development for 2011 and 2012 at Fowler (14.7°C and 15.3°C) relative to College Station (21.1°C) , based on averages of March and April mean temperatures (Appendix 7). Both date of ripening and FDP had low narrow sense heritability estimates (h^2 = 0.07 and 0.06 respectively) (Table 8). This was very surprising considering that much higher estimates of heritability have been reported for both ripening date (h^2 = 0.79 to 0.94) (Hansche et al., 1986; Hansche et al., 1972; de Souza et al., 1998b) and fruit development period (0.73 to 0.98) (Monet and Bastard, 1982; de Souza et al., 1998b; Vileila-Morales et al., 1981). It is important to note that broad sense heritability estimates were very high for the date of ripening and FDP (H^2 = 0.92 and 0.91, respectively) (Table 8). Although the additive genetic component accounted for approximately 4% and 3% of the total phenotypic variance for ripening

date and FDP, the non-additive genetic component was responsible for approximately 51% and 44% of the variance for ripening date and FDP, respectively (Table 8). This discrepancy between the two estimates suggests that a strong non-additive genetic component may have masked the effects of the additive genes for these traits (Bernardo, 2010). Nevertheless, rapid genetic improvement should be possible for both of these traits, given their high genetic variability, if the major genes can be selected for.

Substantial variability was observed for pubescence as indicated by the wide range (zero to seven on a zero to nine scale) with a mean of 3.48 among progeny (Table 6). These measures were similar to that among parents (zero to six on a zero to nine scale) (Table 7). Among peach genotypes, pubescence typically ranged from three to five. Variability might have been lower because the peach parents used in this study were the product of breeding programs in which selection against fuzzy fruit had been practiced for many generations. The nectarine phenotype has a major effect on pubescence, resulting in in the absence of fuzz and is inherited as a single recessive gene (Blake, 1932). Much of the variability observed was due to the effect of nectarine genotypes being scored as zero. In fact, the removal of nectarine seedlings from the analysis resulted in approximately 68% lower phenotypic variance as well as lower additive variance for fruit pubescence (Table 10). Overall, pubescence showed moderate additive inheritance ($h^2 = 0.40$), while the broad sense estimate ($H^2 = 0.94$) (Table 7) would suggest major gene action, based on analysis with all genotypes. The moderate heritability and appreciable variability associated with pubescence should allow for genetic improvement of this trait.

Substantial variability was associated with fruit red blush as indicated by the wide range (1.0 to 5.0 on a zero to five scale) with a mean of 2.97 among progeny (Table 6). Both the range and mean (2.97) among parents were very similar to that of progeny (Table 7). Blush was subject to a strong genotype x environment interaction explaining approximately 58% of total phenotypic variance (Table 8). Fruit red blush was estimated to have moderate additive inheritance ($h^2 = 0.46$) (Table 8). This value was intermediate between those reported previously for this trait (0.41; 0.68) (Hansche and Beres, 1980; de Souza et al. 1998b). Although red blush has been reported to be quantitative (Blake, 1932; Blake, 1940; Hansche, 1986; Weinberger, 1944), recent studies have suggested the presence of major genes (Beckman and Sherman, 2003; Beckman et al., 2005; Frett, 2012). The possible existence of such major genes, particularly the one described by Frett (2012), along with the large variability observed in this population should allow for genetic improvement.

Substantial variability was associated with fruit weight as evident in the higher range of fruit weight among progenies (12.0 to 250.0 grams) (Table 6) compared to the parents (43.0 to 175.0 grams) (Table 7). Fruit in Fowler were approximately 31% and 18% heavier in 2011 and 2012 than in College Station in 2012 (Table 9) and this environmental effect was responsible for approximately 41% of the variation. However there were also substantial changes in rank across these environments and the genotype x environment effect for fruit weight accounted for 44% of phenotypic variance (Table 8). The narrow sense heritability estimate ($h^2 = 0.15$) (Table 8) for fruit weight was lower than the previously reported moderate estimates ($h^2 = 0.32$ to 0.60) (de Souza et al.,

1998b; Hansche, 1986; Monet and Bastard, 1982), although broad sense heritability was estimated as being much higher (H^2 = 0.72) (Table 8). Non-additive genetic variance component accounted for approximately 38% of phenotypic variance compared to only 8% (Table 8) for the additive genetic component, and distribution of fruit weight was also skewed toward the lower end (Appendix 17). This, in conjunction with the high non-additive variance (Table 8), suggests dominance for smaller fruit in these populations as suggested earlier (Connors, 1923; Blake, 1940). Nonetheless, the large amount of variability should allow for steady genetic improvement through recurrent selection and carefully planned crosses.

Fruit diameter displayed transgressive segregation in several progenies (Tables 6 and 7) suggesting substantial genetic variability for this trait. Similar to fruit weight, the genotype x environment effect explained approximately 38% of the phenotypic variance (Table 8). Fruit diameter was found to be moderately heritable (h^2 = 0.45) (Table 8) which was higher than previously reported (h^2 = 0.29; 0.38) (Hansche et al., 1972; de Souza et al., 1998b). The broad sense estimate was approximately twice that of the narrow sense estimate for this trait (Table 8), indicating important non-additive effects. This moderate level of heritability should allow for genetic improvement, although fruit weight had greater variability in spite of its lower level of heritability. Fruit diameter is highly correlated with fruit weight (de Souza et al., 1998) and is generally the easier trait to measure, especially in the case of large samples. Fruit diameter's moderate level of heritability (h^2 = 0.45) (Table 8) should allow for better genetic improvement than fruit

weight. Although fruit weight had greater variability the higher heritability of fruit diameter means that the measurement is more accurate and repeatable.

Fruit tip and fruit shape both showed moderate to substantial variability as indicated by the broad range of scores observed for both traits (5 to 9 on zero to nine scale) with means of 7.71 for fruit tip and 7.28 for fruit shape among progeny (Table 6). These measures varied slightly from that of the parents (6 to 9 on a zero to nine scale) for both traits (Table 7). Both of these traits were affected by a genotype x environment effect that was responsible for approximately 46% and 69% of the total variance for tip and shape, respectively (Table 8). Moderate narrow sense heritability estimates were found for fruit tip ($h^2 = 0.42$) and fruit shape ($h^2 = 0.38$) (Table 8). These estimates were slightly lower than reported earlier ($h^2 = 0.45$ and 0.43, respectively) for fruit tip and fruit shape by de Souza et al., (1998b). Despite the modest amount of variability exhibited for these two traits genetic advance should be possible, but probably slow as reported earlier (de Souza et al., 1998b).

2.4.2 Genotype by environment interactions

As mentioned earlier, several traits were affected by a strong genotype x environment (GxE) interaction. GxE interaction has been described as differential response of genotypes to the environment in which they are grown (Bernardo, 2010). If such interactions exist in the case of specific genotypes across specific environments, selection on the basis of performance for a given trait cannot be practiced in one environment if the plant is expected to perform the same in another (Allard and

Bradshaw, 1964). A stability analysis plotting progeny means across environments was generated to make this comparison easier (Appendices 8 through 12).

Fruit red blush was strongly affected by GxE interaction that was responsible for approximately 58% of total phenotypic variance (Table 8). On average, fruit had approximately the same amount of red blush at Fowler in 2011 and College Station in 2012, but approximately 5% less blush at Fowler in 2012 (Table 9). Two families, both of which had TX2B136 as common parents did not follow this trend, resulting in the interaction (Appendix 8).

Fruit size, measured in two ways, was subject to a genotype x environment effect that accounted for approximately 44% and 38% of the total variance for fruit weight and fruit diameter. (Table 8). Both measures of mean fruit size decreased across all three environments, with the Fowler-2012 and College Station-2012 environments reporting approximately 90% and 76% lower fruit weights, respectively, than Fowler-2011. Decreases in fruit diameter of approximately 1% and 6% were observed for Fowler-2012 and College Station-2012 environments relative to the most favorable environment - Fowler in 2011 (Table 9). The trend for smaller size observed in the second year at Fowler appeared to be related to the higher yield, while the smaller size at College Station was most likely a result of less favorable environmental conditions such as shorter FDP (Table 9) resulting from warmer temperatures during fruit development (Appendix 7). Three families strongly deviated from the above described trend for both measures of size, and the response appeared to be related to parentage (Appendices 9 and 10). All three families shared either TX2B136 or Y434-40 as common parents.

The strong GxE interaction associated with fruit tip and fruit shape was responsible for approximately 46% and 68% of the total variance for these traits (Table 8). Mean fruit tip rating gradually decreased from Fowler-2011 to Fowler-2012 and then decreased more rapidly from Fowler-2012 to College Station-2012, whereas mean fruit shape rating was lower from Fowler-2011 to Fowler-2012, but higher at College Station in 2012 (Table 9). Both fruit tip and shape appearance become less desirable when fruit are exposed to lower chilling conditions and warm temperatures during the early part of development (de Souza et al., 1998b). A comparison of mean monthly temperatures for all three environments revealed that temperatures were slightly warmer at Fowler in 2012 than 2011, and much warmer at College Station in 2012 during bloom and early fruit development (Appendix 7), which might explain why fruit tip ratings were lower for Fowler in 2012 and even lower at College Station in 2012, but not for fruit shape, which had a higher rating at College Station in 2012 due to less prominent sutures, despite receiving lower chilling and higher temperatures during fruit development. Much of the interaction for fruit tip appeared to result from of two families (progenies 7 and 9), which deviated strongly from the overall trend mentioned above, although few individuals were observed for progeny 9 at College Station (Appendix 11). Progeny 7 also appeared to be the source of much of the interaction for fruit shape, as it deviated from the trend mentioned above by performing consistently more poorly across the three environments (Appendix 12).

2.4.3 Major gene effects on heritability

Two major genes - pantao and nectarine can have strong pleiotropic effects on several traits related to fruit quality in peach including smaller size, rounder tip, and greater red blush (Wang, 2009; Wang et al., 2010; Wen et al., 1995a; 1995b; Wu et al., 2003a; 2003b). Nectarine is inherited as a single recessive gene and produces fruit without pubescence (Blake, 1932). Pantao is inherited as a single dominant trait producing flattened or saucer-shape fruit (Scorza and Sherman, 1996). Because several of these progenies were segregating for one or both of these traits, the analysis was run without pantao, nectarine, or both types of seedlings to assess their influence on the heritability, particularly for pubescence, red blush, weight, diameter, and tip. Approximately 15% fewer data points were included with the exclusion of nectarine and approximately 7% fewer without pantao seedlings.

Both narrow sense and broad sense estimates were much lower for pubescence ($h^2 = 0.28$ and $H^2 = 0.54$, respectively) (Table 10) as expected when nectarine genotypes were excluded, likely due to the loss of the lower extreme nectarine types, which were scored as zero. Narrow sense heritability for fruit red blush was also lower ($h^2 = 0.36$) (Table 10) with the removal of nectarine genotypes, was also expected, as nectarines typically tend to have higher red blush (Wang et al., 2010; Wen et al., 1995a; 1995b).

The pantao shape and the nectarine skin type, both conditioned by single genes, are reported to result in smaller fruit as compared to non pantao peaches (Oberle and Nicholson, 1953; Wang, 2009; Wang et al., 2010; Wen et al., 1995 a; 1995b; Wu,

Table 10. Variance component, broad sense heritability (H^2), and narrow sense heritability (h^2) for fruit pubescence and fruit red blush evaluated for two years at Fowler, CA and for one year at College Station, TX comparing the effect of the removal of nectarine, pantao, and both types of seedlings.

Trait [w]	Variances[y]						H^2	h^2
	V_A	V_{DI}	V_G	V_E	V_{GxE}	V_P		
Fruit pubescence	1.52	2.02	3.54	0.1	0.73	3.43	0.94	0.40
Fruit pubescence[p]	1.16	1.41	2.57	0.12	0.75	3.44	0.91	0.41
Fruit pubescence[n]	0.14	0.13	0.27	0.15	0.68	1.10	0.54	0.28
Fruit pubescence[pn]	0.13	0.14	0.27	0.17	0.69	1.13	0.54	0.26
Fruit red blush	0.18	0.08	0.26	0.02	0.40	0.71	0.66	0.46
Fruit red blush[p]	0.18	0.09	0.27	0.02	0.39	0.68	0.68	0.45
Fruit red blush[n]	0.11	0.07	0.18	0.04	0.37	0.59	0.59	0.36
Fruit red blush[pn]	0.11	0.08	0.19	0.04	0.37	0.60	0.61	0.35

[y]V_A = additive genetic variance; V_{DI} = non-additive genetic variance; V_G = genetic variance (additive and non-additive); V_E = environmental variance; V_{GxE} = genotype x environmental variance; V_P = phenotypic variance.

[w]fruit pubescence visually based on 0-9 scale (0 = no pubescence, 6 or higher = greater pubescence than modern cultivars); fruit red blush visually based on % coverage of red blush on skin using 0-5 scale (0 = 0% red coverage, 1 = 1%-20%, 2 = 21%-50%, 3 = 51%-80%, 4 = 81%-99%, 5 = 100%)

[p]Analysis run without pantao seedlings.

[n]Analysis run without nectarine seedlings.

[pn]Analysis run without both pantao and nectarine seedlings.

Table 11. Variance component, broad sense heritability (H^2), and narrow sense heritability (h^2) for fruit weight and fruit diameter evaluated for two years at Fowler, CA and for one year at College Station, TX comparing the effect of the removal of nectarine, pantao, and both types of seedlings.

Trait[w]	Variances[y]						H^2	h^2
	V_A	V_{DI}	V_G	V_E	V_{GxE}	V_P		
Fruit weight	96.59	358.62	455.21	217.95	528.81	1201.96	0.72	0.15
Fruit weight[p]	181.52	329.91	511.43	243.55	525.20	1280.19	0.74	0.26
Fruit weight[n]	-0.38	316.16	315.78	263.12	582.65	1163.92	0.62	0.00
Fruit weight[pn]	148.19	323.18	471.37	310.85	565.82	1348.06	0.71	0.22
Fruit diameter	17.64	14.16	31.62	4.63	21.83	58.08	0.81	0.45
Fruit diameter[p]	11.25	13.48	24.73	4.81	21.39	50.93	0.78	0.35
Fruit diameter[n]	8.95	11.34	20.29	5.40	24.15	49.85	0.72	0.32
Fruit diameter[pn]	2.91	11.20	12.82	5.38	23.56	43.06	0.62	0.14

[y]V_A = additive genetic variance; V_{DI} = non-additive genetic variance; V_G = genetic variance (additive and non-additive); V_E = environmental variance; V_{GxE} = genotype x environmental variance; V_P = phenotypic variance.

[w]fruit weight in grams; fruit diameter in millimeters.

[p]Analysis run without pantao seedlings.

[n]Analysis run without nectarine seedlings.

[pn]Analysis run without both pantao and nectarine seedlings.

Table 12. Variance component, broad sense heritability (H^2), and narrow sense heritability (h^2) for fruit tip and shape evaluated for two years at Fowler, CA and for one year at College Station, TX comparing the effect of the removal of nectarine, pantao, and both types of seedlings.

Trait [w]	Variances[y]						H^2	h^2
	V_A	V_{DI}	V_G	V_E	V_{GxE}	V_P		
Fruit tip	0.18	0.13	0.31	0.12	0.36	0.79	0.72	0.42
Fruit tip[p]	0.18	0.09	0.27	0.12	0.35	0.75	0.70	0.47
Fruit tip[n]	0.12	0.12	0.24	0.14	0.38	0.75	0.65	0.33
Fruit tip[pn]	0.10	0.07	0.17	0.13	0.37	0.67	0.58	0.34
Fruit shape	0.09	0.02	0.11	0.07	0.39	0.57	0.46	0.38
Fruit shape[p]	0.10	0.02	0.12	0.08	0.37	0.57	0.49	0.41
Fruit shape[n]	0.09	0.01	0.10	0.07	0.39	0.55	0.43	0.39
Fruit shape[pn]	0.08	0.02	0.10	0.08	0.36	0.45	0.45	0.36

[y]V_A = additive genetic variance; V_{DI} = non-additive genetic variance; V_G = genetic variance (additive and non-additive); V_E = environmental variance; V_{GxE} = genotype x environmental variance; V_P = phenotypic variance.

[w]fruit tip visually based on 0-9 scale (6 or lower = very prominent fruit tip, 9 = completely oblate fruit tip); fruit shape visually based on 0-9 scale (6 or lower = large suture bulge and prominent tip, 9 = no pronounced suture and oblate tip).

[p]Analysis run without pantao seedlings.

[n]Analysis run without nectarine seedlings.

[pn]Analysis run without both pantao and nectarine seedlings.

2003b). Additive variance was approximately twice as great and narrow sense heritability was slightly higher ($h^2 = 0.26$) for fruit weight with the exclusion of pantao genotypes from the analysis (Table 11). Pantao fruit are typically lighter than round fruit (Wang, 2009; Wang et al., 2010). Additive variance and narrow sense heritability for weight were reduced to zero with the exclusion of nectarines (Table 10). This was possibly a result of the decreased variability resulting from the removal of nectarines, which tend to be smaller (Oberle and Nicholson, 1953; Wang, 2009; Wang et al., 2010; Wen et al., 1995a; 1995b; Wu, 2003b). Narrow sense heritability for fruit diameter was slightly lower when either pantao ($h^2 = 0.35$) or nectarine ($h^2 = 0.32$) genotypes were excluded, and was much lower ($h^2 = 0.14$) when both genotypes were excluded from the analysis. Again, the broad sense estimate was about twice that of the narrow sense heritability estimate for diameter (Table 11).

Additive inheritance for fruit tip was lower ($h^2 = 0.33$ when nectarines were excluded. Nectarines tend to be rounder with less pronounced tips (Wang, 2009), the removal of which appears to have decreased additive variance for this trait by approximately 33% (Table 12).

2.4.4 Phenotypic correlations

It is important to remember that because phenotypic correlations are an estimate of the relationship between the two traits based on both environmental and genetic factors, thus their usefulness is limited (de Souza et al., 1998a). In addition, phenotypic correlation is mostly a function of environmental correlations when heritability is low

for a given trait (Falconer, 1989). The ultimate application for inter-trait correlation in plant breeding is indirect selection (Searle, 1965). Correlations were computed on a pair-wise basis for all traits. Significance of correlation estimates were discussed based on the magnitude of the estimate because the sampling variances for the correlation estimates were not available (de Souza et al., 1998a). Thus correlation estimates of ≥0.65, between 0.50 and 0.64, and between 0.30 and 0.49 were deemed as strong to very strong, moderately strong, and moderately weak, respectively. Estimates of ≤0.29 were considered weak and will not be discussed.

Date of ripening was highly correlated (r = 0.94) (Table 13) with FDP, suggesting that it is a more reliable predictor of FDP than bloom date (de Souza et al., 1998b) as the correlation with FDP was stronger for date of ripening compared to bloom date. Date of bloom was negatively correlated (r = -0.45) (Table 13) with FDP, suggesting that the early development period of fruit is delayed by cooler temperatures (Weinberger, 1948; Boonprakob et al., 1992; de Souza et al., 1998b). Not surprisingly, the correlation estimate for fruit weight and fruit diameter was very strong (r = 0.83) (Table 13) reaffirming the fact that both traits are an acceptable measure of size in fruit and can be used interchangeably in a selection program as discussed earlier. In fact, this estimate was even higher (r = 0.90) (Appendix 1) when lighter and wider pantao genotypes were removed from the analysis, supporting the conclusion that pantao fruit tend to be lighter than round fruit with the same diameter (Wang, 2009; Wang et al., 2010).

Table 13. Phenotypic correlations among nine peach tree and fruit quality traits evaluated for two years at Fowler, CA and one year at College Station, TX.[z]

Characters[y]	Bloom	Ripe	FDP	Pub.	Blush	Weight	Diam.	Tip	Shape
Bloom	---	-0.16	-0.45	0.31	0.05	-0.09	-0.07	-0.40	-0.24
Ripe	-0.16	---	0.94	0.08	-0.31	0.54	0.55	0.05	0.04
FDP	-0.45	0.94	---	-0.02	-0.38	0.50	0.51	0.16	0.08
Pubescence	0.31	0.08	-0.02	---	-0.04	0.26	0.22	-0.28	-0.22
Blush	0.05	-0.31	-0.38	-0.04	---	-0.24	-0.24	0.04	0.18
Weight	-0.09	0.54	0.50	0.26	-0.24	---	0.83	-0.04	0.07
Diameter	-0.07	0.55	0.51	0.22	-0.24	0.83	---	0.12	0.08
Tip	-0.40	0.05	0.16	-0.28	0.04	-0.04	0.12	---	0.36
Shape	-0.24	0.04	0.08	-0.22	0.18	0.07	0.08	0.36	---

[z]Correlation values $r_p \geq 0.65$; $0.64 \geq r_p \geq 0.50$; $0.49 \geq r_p \geq 0.30$; $r_p < 0.30$ were considered strong or very strong, moderately strong, moderately weak, and weak or very weak, respectfully. Correlation values ≥ are underlined.

[y]Date of full bloom and date of ripening expressed in Julian Days; fruit development period in days; fruit pubescence visually based on 0-9 scale (0 = no pubescence, 6 or higher = greater pubescence than modern cultivars); fruit red blush visually based on % coverage of red blush on skin using 0-5 scale (0 = 0% red coverage, 1 = 1%-20%, 2 = 21%-50%, 3 = 51%-80%, 4 = 81%-99%, 5 = 100%); fruit weight in grams; fruit diameter in millimeters; fruit tip visually based on 0-9 scale (6 or lower = very prominent fruit tip, 9 = completely oblate fruit tip); fruit shape visually based on 0-9 scale (6 or lower = large suture bulge and prominent tip, 9 = no pronounced suture and oblate tip.

The correlations of fruit red blush with date of ripening (r = -0.31) and FDP (r = -0.38) (Table 13), although reported earlier (de Souza et al., 1998b) were relatively weak. This may also be the result of later ripening fruit developing less skin color due to a denser tree canopy later in the season. Fruit positioned deep in the tree canopy have less red blush (Bible and Singha, 1993; Lewallen and Marini, 2003). Both date of ripening and FDP were positively correlated with fruit weight (r = 0.54 and 0.50) (Table 13). Fruit diameter was also positively correlated with ripening date and FDP (r = 0.55 and 0.51) (Table 13) suggesting that the later a fruit is on tree, the more resources can be sequestered and allocated to it.

Fruit tip and fruit shape exhibited a moderately weak correlation (r = 0.36) (Table 13), which was much lower than previously reported by de Souza et al., (1998b). This relationship is not unexpected considering that the subjective scale used to evaluate fruit shape largely reflects both the tip rating and the appearance of the suture bulge. Values between these two traits were lower (r = 0.31) when nectarine genotypes were excluded, and higher (r = 0.41) when pantao genotypes were excluded from the analysis (Appendix 1). This was probably a result of nectarines generally having rounder tips and pantao receiving high tip ratings in spite of low ratings for overall shape because of irregular sutures. The negative correlation between bloom date and fruit tip (r = -0.40) (Table 13) supports the conclusion by de Souza et al. (1998b) and Topp and Sherman (1989) that cooler temperatures during early fruit development improve the appearance of fruit tip.

The correlation of 0.31 (Table 13) between bloom date and pubescence was moderately weak, at best, and was much lower (r = 0.08) (Appendix 2) when nectarine genotypes where not considered. The progenies that segregated for nectarine were generally earlier blooming, and this was more likely a result of the genetic background of the nectarines and not a pleiotropic effect of the nectarine gene itself.

2.5 Conclusions

All traits evaluated were associated with large phenotypic variability, while fruit tip and fruit shape exhibited more moderate measures of variability. Variability is a major component in the estimation of heritability, and both are necessary for genetic improvement. Most traits were estimated to be moderately heritable on a narrow sense basis, while two showed low and one showed high additive inheritance. Given the appreciable variability and moderate heritability, some genetic advance should be possible for most traits evaluated. Heritability and genetic correlations are dependent on the specific germplasm and environments used in each investigation and the results of this study differ from some previous studies.

Date of full bloom was highly heritable (h^2 = 0.62) on a narrow sense basis, whereas date of ripening and FDP were associated with low heritability in spite of being widely reported as highly heritable traits. Broad sense estimates for these traits were high, suggesting an important non additive genetic component. Contrary to previous studies, fruit weight also showed low additive inheritance, although the broad sense

heritability was also high for this trait. Distribution of fruit weight was negatively skewed, suggesting dominance for small fruit size.

Moderate narrow sense heritability was associated with all the other traits (fruit pubescence, fruit red blush, fruit diameter, fruit tip, and fruit shape) as expected from previous studies. Heritability ranged from 0.38 for fruit shape to 0.46 for fruit red blush.

Most traits were not strongly influenced by environment: however, date of full bloom, date of ripening, and FDP showed major differences across environments mainly due to temperature differences among environments. Trees typically bloomed earlier and fruit ripened later and over a longer period of time at Fowler than at College Station.

Several traits were subject to strong genotype x environment effects, suggesting that, for these traits, selection should only be practiced where the plants are intended to be grown. Fruit red blush, fruit weight, fruit diameter, fruit tip, and fruit shape showed differential response with respect to genotype across different environments. For each trait, the interaction appeared to be the result of one or two progeny families behaving differently from the general trend across environments.

Several progenies were segregating for two major genes, pantao and nectarine, which have been reported to have pleiotropic effects on fruit size, fruit red blush, and shape, thus analysis was run without pantao, nectarine, and both types of seedlings for these traits. Removal of nectarine seedlings from the analysis resulted in lower heritability estimates for fruit pubescence, fruit red blush, fruit weight, and fruit tip. Heritability for fruit weight was higher with the removal of pantao seedlings, while fruit diameter showed a lower value when both pantao and nectarine were removed. The

exclusion of nectarine and pantao seedlings from the analysis resulted in approximately 15% and 7% fewer data points for these traits. Overall, heritability was not strongly affected by these major genes, except in the case of fruit pubescence, which went from moderate to low heritability (h^2) with the exclusion of nectarine seedlings as well as fruit diameter, which had the same response with the removal of both pantao and nectarine seedlings from the analysis.

The ultimate implication of high correlations between traits is in the ability to practice indirect selection. Because phenotypic correlations were based on relationships between traits based on both genetic and environmental factors, their usefulness would be limited, especially when heritability is low for both related traits. None of the correlations were strong enough among traits to allow for selection for multiple traits, as most relationships were the result of environmental or physiological relationships, or were simply different measures of the same trait.

Date of ripening and FDP were strongly correlated (r = 0.94), suggesting that ripening date is a reliable estimator of FDP. The negative correlation between date of full bloom and FDP (r = -0.45) suggests that earlier blooming during cool temperatures tends to extend fruit development period. The moderately weak negative correlations of fruit red blush with date of ripening (r = -0.31) and FDP (-0.38) were most likely a function of decreased blush caused by lower light exposure of fruit due to denser tree canopy later in the season. Date of full bloom and fruit tip were moderately and negatively correlated (r = -0.40) as reported previously, as earlier blooming seedlings

tend to produce rounder tip fruit in response to cooler temperatures during bloom and early development.

Fruit weight and fruit diameter were moderately strongly correlated with date of ripening (r = 0.54; 0.55) and FDP (r = .50; 0.51) respectively. As previously reported, fruit size tends to increase as fruit ripens later as a result of greater resources available for growth.

Fruit weight and fruit diameter were strongly correlated (r = 0.83) as expected, suggesting that both are reliable measures of fruit size. Fruit tip and fruit shape were moderately weakly correlated (r = 0.36) which was not surprising considering that overall fruit shape is partially a representation of fruit tip, and was weaker without rounder tip nectarines and stronger without pantao, which received high tip ratings, but often lower ratings for fruit shape based on irregular sutures.

CHAPTER III

HERITABILITY AND PHENOTYPIC CORRELATIONS RELATING TO SEVERAL FRUIT QUALITY TRAITS IN PEACH

3.1 Synopsis

Six peach [*Prunus persica* (L.) Batsch] fruit quality traits were evaluated for two years at Fowler, CA and one year at College Station, TX to estimate heritability and phenotypic correlations. Seedlings from nine F_1 families were budded onto 'Nemaguard' rootstocks along with the parents for evaluation. Variance components were estimated using an all random effects model (REML) and a multivariate model was used to estimate phenotypic correlations between traits. Moderate to high heritability was estimated for ground color (h^2 = 0.50), while red in the flesh, firmness, soluble solids, titratable acidity (TA), and pit weight showed low heritability (h^2 = 0.05-0.24). In contrast, the traits with low additive heritability showed moderate to high broad sense heritability (H^2) indicating a significant non additive genetic component. Several traits (fruit ground color, red in the flesh, fruit firmness, and soluble solids) were strongly influenced by genotype by environment effects. A large amount of phenotypic variability was associated with fruit firmness, soluble solids, and TA, which should allow for genetic improvement of these traits. All significant correlations were between the six traits and those discussed in the previous paper. Soluble solids was moderately weakly correlated with ripe date and fruit development period (FDP) (r = 0.32, r = 0.33). Pit weight was moderately correlated with FDP, fruit weight, and fruit diameter (r =

0.33, r = 0.51, r = 0.31, respectively). None of the relationships represented by the correlations were strong enough to be taken advantage of in a multiple trait selection program.

3.2 Introduction

The objectives of this research were to determine:

1) Variance components of several fruit quality traits including fruit ground color, red in flesh, fruit firmness, soluble solids, titratable acidity (TA), and pit weight.
2) Estimates of heritability in the narrow sense (h^2) and broad sense (H^2) for the above mentioned traits.
3) Genetic and phenotypic correlations among fruit quality traits.

3.2.1 Review of literature relating to fruit quality traits

Of all the biochemical compounds and physical attributes that affect quality, sugar content is unrivaled in its impact on fruit quality. Soluble sugars are attributed to many fruit quality traits such as flavor, as well as metabolism and overall nutrition (Cantin et al., 2009). Generally, high consumer acceptance is related to high soluble solid concentration (SSC) in peaches (Crisosto and Crisosto, 2005). Recent surveys have suggested that soluble solids levels must be greater than 10% for acidic cultivars and 11% for low acid peaches/nectarines in order to be considered acceptable to consumers (Crisosto et al., 2003). The organoleptic quality of fleshy fruits is most strongly affected

by the content and composition of soluble sugars and organic acids (Dirlewanger et al., 1999). Peaches contain several major sugars including sucrose, fructose, glucose, and sorbitol, with sucrose the most abundant (Cantin et al., 2009; Dirlewanger et al., 1999; Byrne, et al., 1991).

Sugar content in peach, as measured by soluble solids concentration (SSC) is quantitatively inherited with heritability estimates ranging from low (h^2=0.01) (Hansche et al., 1972) to moderate (h^2 = 0.33; 0.43) (de Souza et al., 1998; Monet and Bastard, 1982) to high, at over 0.72 (H^2) (Brooks et al., 1993). SSC is influenced by the conditions under which the plant is grown, including: amount of light received, canopy position, available water during fruit development, plant nutrition, thinning practices, position in canopy, and temperature during fruit development (Westwood, 1993). Although sugar content will receive the most focus in this investigation, there are many traits that affect quality in peach.

As with the development of new varieties for other crops, it is difficult to find a genotype that combines all the desirable traits. Both size and soluble solids are generally lower for peaches and nectarines with shorter fruit development periods, making development of early ripening cultivars that also have high quality difficult (de Souza et al., 1998b; Wu et al., 2003). There can also be interactions between qualitative and quantitative traits. For example, nectarines and flat fruits showed a tendency of having higher SSC and total sugar content than peaches and round fruits, respectively (Cantin et al., 2009; Wang et al., 2010; Wen et al., 1995). Soluble solids had a negative genetic correlation with fruit mass (Wu et al., 2003). Red blush had a moderately weak and

negative phenotypic correlation with soluble solids (r = -030), although the genetic correlation was stronger (r=-0.56) (de Souza et al., 1998b).

With regard to organoleptic quality, titratable acidity is probably the second most important component in peach after SSC (Crisosto, 2005). The sugar/acid ratio is an essential component of the organoleptic quality for fruits in the Rosaceae family. Expression of acidity in peach appears to be controlled by a single gene *D* that is completely dominant for low acid in peach (Dirlewanger et al., 2009). The *D* gene, controlling the non-acid trait in peach, is dominant and segregates as a Mendelian character (Boudehri et al., 2009). Wide variation within acid type progenies, however, suggests that the amount and type of acidity is under quantitative genetic control. Levels of specific acids such as malic, citric, and quinic vary widely (Byrne et al., 1991), and chemical analysis of these specific acids and sugars can aid in determining peach fruit quality (Colaric et al., 2005). Total acidity was reportedly higher in nectarine when compared to peach siblings (Wen et al., 1995a; 1995b) or within a germplasm collection (Wang, 2009). Heritability estimates for titratable acidity range from low ($h^2 \leq 0.19$) (Hansche, 1986; Hansche and Beres, 1980; Hansche et al., 1972) to moderate ($h^2 = 0.31$) (de Souza et al., 1998b)

Adequate fruit firmness is as absolute requirement for new commercial varieties of peach (Byrne, 2005), in order to allow for harvest at a later maturity level so that other fruit quality traits are not diminished (Hough, 1985). Both the stony-hard and non-melting flesh types are inherited as single genes (Haji et al., 2005). Recently, endoPG has been identified as the major enzyme responsible for cell wall degradation and

eventual melting. The study on the effects of pleiotropy of nectarine and pantao traits reported that firmness was considerably lower among genotypes that express the flat pantao trait (Wang, 2009), while nectarines had greater flesh firmness and were reportedly denser (Wang, 2009; Wen et al., 1995a). The heritability of flesh firmness among melting genotypes is reportedly low ($h^2 = 0.13$) (Hansche et al., 1972).

Ground color, closely related to flesh color, is a result of chlorophyll, carotenoids, anthocyanins, and other pigments (Lancaster and Lister, 1997), with carotenoids being the primary factor determining flesh color (Flesh color type, whether white or yellow, appear to have no effect on either titratable acidity or soluble solids (Wu, 2003). Green on the skin of mature fruit for fresh market use is undesirable. Ground color is also often used as a major determinant for harvest time of peach (Lewallen and Marini, 2003). Flesh color under the skin appears to be controlled by two genes resulting in white, yellow, and red phenotypes (Iezzoni, 1983). Recently, both concentration and distribution of red anthocyanins and carotenoids in the flesh and around the pit have been reported to be regulated by several genes at the 'Cs' locus (JiCheng et al., 2012).

Pit weight is closely related, but not necessarily proportional to overall fruit weight (Chalmers and van den Ende, 1975), and large pit size is generally undesirable. Although pit size is appears to be under quantitative control, with no discrete categories among stone sizes, dominance of large stone size has been observed among crosses between some cultivars (Hesse, 1975). More recently, evidence suggesting the possible existence of a few major dominant genes has been reported (Bassi et al., 1989). Pit size

and fruit size are closely related, but not necessarily proportional to one another (Chalmers and van den Ende, 1975).

Freestone and clingstone appear to segregate as a single loci, (Janick and Moore, 1975), although intermediate phenotypes also exist. While the degree of adherence in these intermediate phenotypes has been reported to be seasonally influenced, it is possible that additional modifying genes also exist. Non-melting flesh type appears to be inherited with clingstone without fail, while most freestone fruit are also of the melting flesh type, although melting flesh fruit that are clingstone are not uncommon (Okie, 1998).There has been debate for some time as to whether the often-associated freestone and melting traits are controlled by a single locus, or are closely linked. A recent molecular study suggests that the freestone and melting genes are located at the same locus and that there may be three alleles for the three phenotypic classes (Peace, et al., 2005).

3.2.2 Variance component and heritability

Overall peach fruit quality is a complex trait that is affected by genetics, the environment, environmental interaction with genetics, and cultural practices (Byrne, 2005; Crisosto et al., 1997). When selecting for superior cultivars, it is important to better understand all forces that contribute to the phenotype of the plant, as well as how they interact. Elementary Yield, fruit size, tree productivity, and other traits are reported to be under polygenic control. At present, many of these traits appear to have low heritability (Sansavini et al., 2006), which might be overcome by increasing variability

through introgression of new material with greater relative variability for a particular trait.

An understanding of genetic parameters including variances, heritability, and relationships among traits can be very useful when attempting to make predictions of genetic progress over generations, particularly when selection of parents is based on their own performance (Falconer, 1989). One of the most important genetic concepts dealing with breeding is heritability, which partitions the genetic contribution to a plant's phenotype from environmental effects. This will be a focus of this study.

Estimates of heritability can be used for predicting genetic progress for progeny when selection of parents is based on based on their own performance (de Souza et al., 1998a). Some traits appear to be highly heritable, so that they can be reliably and accurately measured, such that expression of such traits is not heavily influenced by differential interaction effects with the environment, while others have low heritability (Moing et al., 2003). Examples of highly heritable fruit quality traits in peach are: the percentage of skin red blush ($h^2 = 0.68$) (de Souza et al., 2000), the date of ripening ($h^2 = 0.94$) and fruit development period (FDP) ($h^2 = 0.91$) (de Souza et al., 1998b). Most studies on quantitative traits in peach have focused mainly on narrow-sense heritability (de Souza et al., 1998a) which considers only additive genetic variation and is most valuable to the breeder for making gains through selection. While these and other previously conducted studies have reported heritability and combining abilities in the case of tree fruit crops, most have consisted of progenies being evaluated on their own roots in the same location for multiple years.

Although earlier studies have arrived at heritability estimates by interpreting the genetic variance of a given progeny based on the covariance among relatives , recent studies have focused on estimating heritability on a progeny-mean basis expressed as the proportion of genetic (V_G or V_A) variance among a progeny to that of the phenotypic variance (V_P) (Bernardo, 2010). Linear regression of offspring performance on mid-parent performance has also been a useful method (Falconer, 1989), but is only an accurate estimate when the inbreeding coefficient is equal to zero (Fernandez and Miller, 1985). Although other methods of analysis based on variance components have been used, most require robust experimental designs with reciprocal crossing and replications-all of which have limited feasibility in tree crops (de Souza, 1996).

Random effects models such as restricted maximum likelihood (REML) were developed and first used by animal geneticists (Searle, 1971; Henderson, 1983), and later by plant breeders (Vileila-Morales et al., 1981; McCutchan et al., 1985; Huber, 1994; Tancred et al., 1995). Studies by Vileila-Morales et al. (1981) and de Souza et al., (1998) have thus far been the only examples of using such a model for analyzing variance components in peach. In addition to providing generalized least squares estimation of fixed effects, providing flexibility in model specification for univariate and multivariate forms and correlated residual terms (Henderson, 1974; Huber, 1994), REML has critically proven to provide robust analysis with the use of unbalanced and non-normal data (Banks et al., 1985; Westfall, 1987).

3.2.3 Phenotypic correlations

Phenotypic correlation is determined from raw phenotypic values between two traits and accounts for both genetic and environmental correlations. Phenotypic correlations are mostly a function of environmental correlation when there is low heritability for a given trait (Falconer, 1989). Genetic correlations are primarily due to pleiotropy, but with low recombination are also often the result of linkage. Genetic correlations are more useful when the heritability of the two measured traits is high (de Souza, 1996). Correlations between traits can be especially useful in plant breeding where indirect selection may be applied for a trait. For instance, selecting on a correlated trait that is more easily measured than another highly correlated trait, assuming both traits have moderate to high heritability (Bernardo, 2010). Most correlations studies for peach and other fruit crops in the past have traditionally reported only on phenotypic correlations. It is important to keep in mind that the implication of phenotypic correlation in a breeding program is limited by the fact that both genetic and environmental correlations are included (de Souza et al., 1996). The same methods for estimating variance components such as mixed models can also be applied to calculate both phenotypic and genetic correlations, but parent-progeny models may also be used (Falconer, 1989). Typically, a bivariate analysis is used to compute correlations, and is carried out two traits at a time (Henderson, 1983).

3.3 Materials and methods

3.3.1 Plant material

Three hundred and ninety-six seedlings were randomly selected from nine F_1 families (Tables 14 and 15) created by crossing high sugar selections from the USDA Stone Fruit Breeding Program in Parlier, CA and medium to low chill selections from the Texas A&M University breeding program. The number of seedlings in each family ranged from eight to 90. Parents used for crosses (Table 14) have been shown to vary in the concentration of solids, ranging from 10.7 to 13.0 °Brix, and in chill requirement from approximately 150 to 650 chilling units. Other traits segregating in these progenies include fruit type (peach versus nectarine, round versus flat shape), fruit shape (prominence of tip and suture), fruit color (flesh and skin), fruit size, bloom date, ripe date, productivity, and fruit development period.

Scion wood was collected from the parents and the original seedlings from breeding plots in College Station, TX and Floresville, TX. These were budded onto 'Nemaguard' peach rootstocks in the two evaluation plots in College Station, TX and Fowler, California. Each site included one replicate of each seedling and three to four replicates of each parent.

3.3.2 Plot establishment and design

At the College Station site, one replicate of the propagated seedlings were randomized along with four replicates of each parent in a randomized block design. At the Fowler site plants were grouped according to progeny along with the three to four

Table 14. Characteristics of peach parents used in this study.

Genotype	Fruit type	Date of full bloom	Date of ripening	Fruit red blush	Fruit weight	Fruit diameter	Soluble solids	Titratable acidity	Notes
Y426-371	Ne-Yel	Feb 18	May 28	90	79.3	54.5	12.9	0.41	
Y434-40	Ne-Yel	Feb 6	May 16	70-90	75.6	54.5	12.7	0.44	
Y435-246	Ne-Yel	Feb 22	Jun 12	20-50	63.1	50.3	12.5	0.34	
Galaxy	Pc-Wh	Feb 19	Jun 12	40-70	140.9	76.9	12.6	0.24	Pantao[Y]
Victor	Pc-Yel	Feb 11	May 18	50-70	115.9	64.1	10.7	0.87	
TX2B136	Pc-Yel	Feb 5	Jun 2	60-80	119.8	63.4	11.0	1.29	
TX3E213LW	Pc-Wh	Feb 20	Jun 7	70-80	118.2	62.3	13.0	0.33	
TXW1490-1	Pc-Yel	Feb 5	Jun 8	30-40	107.6	61.9	12.2	1.0	

[Y]Pantao is heterozygous for round shape, homozygous pantao types do not survive

Date of full bloom and date of ripening expressed in days; fruit red blush visually based on % coverage of red blush on skin; fruit weight in grams; fruit diameter in millimeters; soluble solids in °Brix; titratable acidity in Eq H^+/1000 mL of juice

Table 15. Peach crosses and number of individuals evaluated.

Female		Male	Progeny
1	TX2B136	*Y434-40*	71
2	TX2B136	*Y435-246*	30
3	‘Victor’	*Y426-371*	90
4	‘Victor’	*Y435-246*	36
5	‘Victor’	*‘Galaxy’*	36
6	TX2B136	*‘Galaxy’*	50
7	TX3E213LW	*Y434-40*	50
8	TXW1490-1	*Y434-40*	25
9	TXW1490-1	*Y435-246*	8

replicates of each parent.

In both cases, experimental blocks had border trees at the ends of each row and border rows immediately adjacent to the outer two rows. Parental genotypes were replicated to gain a better assessment of the phenotypic variance attributed to environmental effects.

Trees in the College Station plot were planted in staggered double-rows, with trees spaced 1.7 meters apart in double rows (0.67 meters apart). There were five meters between each group of double row (Figure 1 in Chapter II). All trees were trained as central leader.

Trees in the Fresno plot were trained as a two-scaffold 'Y' system and spaced approximately one meter apart in single rows, approximately 4 meters apart. At each location, irrigation, fertilization, pest and weed control, pruning, and fruit thinning were carried out as necessary according to typical commercial practice.

Progenies and parents were evaluated at the two locations over two years (Table 17). Fowler, near Fresno, CA is located in the center of the stone fruit producing San Joaquin Valley in central California and is ideal for peach production with a semi-arid Mediterranean climate. It has long hot, dry summers and mild, wet winters. Fresno receives an average 284 mm rainfall per year, with temperatures ranging from 3.56°C (min. ave. Jan. temp) to 35.89°C (max. July temp.). Fowler receives on average 80% of the total possible sunlight each year (Weather Underground, 2011). Situated in the middle of the Central Valley, the Fresno area has, for the most part, deep, alluvial sandy-loam soils with coarse texture and good internal drainage.

Table 16. A comparison of climate and geography between two sites.

	College Station, Texas	Fresno, California
Location	30°36'5" N, 96°18’52" W	36°44'52" N, 119°46'21" W
Average Elevation	112 m	90 m
Average Annual Rainfall	1000 mm	284 mm
Min. Ave. January Temperature	4.4°C	3.56°C
Max. Ave July Temperature	35.6°C	35.89°C
Ave. sunlight hours received	2578	3550
Climate	Sub-humid/warm temperate	Semi-arid/Mediterranean
Soil	Clay-pan	Alluvial sandy-loam

Data based on historical soil survey (USDA) and historical climate records (Weather Underground, 2011).

College Station, TX is located in East Central Texas where stone fruit production in terms of acreage is comparatively small due to marginal soil and climate. The climate is described as sub-humid and warm temperate with mild winters and warm to hot, humid summers. College Station receives an average of 1000 mm rain per year, with temperatures ranging from 4.4°C (Min. Ave. Jan. Temp.) to 35.6°C (Max. Ave. July Temp.). College Station receives 27% less sunlight in a given year than does Fresno, except during the winter and early spring (Weather Underground, 2011). The College Station area is geographically nearly flat to slightly rolling hills, with the typical topsoil type a shallow moderately coarse sandy-loam to loamy sand with good internal drainage. The region is also plagued with heavy clay subsoil with very poor structure and very limited internal drainage and aeration. The College Station site is plagued with poor quality water for irrigation, with high alkalinity and sodium levels. Compared to Fresno, College Station is much more likely to experience late damaging spring freezes, extreme temperature swings, and inconsistent rainfall (drought or flooding). Less and sporadic amounts of chilling received from year to year as well as warm temperatures during fruit development can also be major problems. The College Station site has higher humidity (favoring disease), warmer night temperatures and lower sunlight during fruit development period; these collectively often result in relatively smaller fruit size, color, and soluble solids compared to the San Joaquin Valley. This overall makes College Station less suitable for stone fruit production and makes it possible for it to be considered a stress environment.

3.3.3 Data collection

Data was collected for two years from the California plot (2011 and 2012) and one year from the Texas plot (2012) (Table 18). A severe drought and slow plant establishment resulted in no data being collected in Texas in 2011. Collection of data at the Texas site was conducted by the Texas A&M Breeding Program. However, at the California site, the bloom data and fruit samples along with maturity data were collected by the staff of The Burchell Nursery where the block was planted. Pictures of each five fruit sample were taken of the exterior of the fruit from four positions: top, cheek (one side), suture, and tip. Pictures were also taken by the Texas A&M Stone Fruit Breeding Program and Fruit Dynamics, Inc. following a combination of transverse and equatorial bisecting cuts revealing the interior of both remaining halves from each of the five cut fruit. Pictures were taken as possible of every entry at both locations.

3.3.4 Qualitative traits

A five fruit sample was used for evaluation of all qualitative traits being visually assessed. If expression of a given trait was not uniform among all fruit in a sample, an average or approximation was recorded. This evaluation took place either inside the TAMU Stone Fruit Breeding lab or inside the Burchell Nursery building at Fowler under normal fluorescent lighting.

Fruit ground color describes the color of the fruit surface not covered by red blush and was visually recorded based on a standard color chart. This color was then assigned to one of the following: white, white-green, green, white-yellow, yellow,

Table 17. Parameters used for evaluation of nine peach fruit quality traits.

Trait:	Parameter:	Units:
Fruit ground color	Visually based on presence of green using 0-2 scale	
Flesh color	Visually based on presence of green using 0-2 scale	
Red in flesh	Visually based on % red overlay using 0-9 scale (0=0%, 1=10%)	
Red around pit	Visually, reported as absent or present (0-1)	
Fruit firmness	Using table mounted penetrometer average five fruits	Pounds of force
Flesh adherence	Visually using 1-4 scale (1=free, 4=cling)	
Soluble solids	Using temperature compensated refractometer, five fruit average	Degree Brix
Titratable acidity	Manually with burette, 0.1 N NaOH to pH 8.1	Eq H^+/1000 mL
Pit weight	Five fruit average	Grams

yellow-green, yellow-orange, orange, red-orange, and red. Fruit flesh color describes the color of the inside of the fruit flesh or mesocarp not overlaid by red pigmentation. The same procedure for color assigning used to describe fruit ground color was used to describe fruit flesh color. Both fruit ground color and fruit flesh color were later classified using a score scale ranging from 0 to 2 to reflect presence of green color in which 0 indicated green color, 1 indicated a combination of green and another color, and 2 indicated no green color.

Red in flesh describes the amount of the cut flesh surface that is overlaid with red pigmentation and was based on a score scale ranging from 0 to 10 in which 0 indicates 0% red overlay and 10 indicates 100% red overlay. Red around pit describes the presence of red pigmentation around the pit or endocarp. Samples were either classified as having red pigmentation present or absent using a binary 0-1 scale.

Flesh adherence was subjectively evaluated on a 1- 4 scale in which a score of 1 indicated complete separation of flesh from endocarp (freestone) and a 4 indicated complete adherence or no separation of flesh from endocarp (clingstone). Scores of 2 and 3 indicate intermediate degrees of flesh adherence, with 2 being closer to freestone and 3 closer to clingstone.

3.3.5 Quantitative traits

Fruit firmness measurements were done using a table-mounted penetrometer based on a five fruit average. A section of fruit peel was removed from the part of each fruit where the instrument tip was inserted to a standard depth into the fruit flesh. Effort

was taken to attempt that all fruit was of uniform maturity. The same procedure was used by the staff at the Fruit Dynamics lab for fruit from the Fowler location as for those from College Station.

Soluble solids data was reported as degrees Brix and was measured using a temperature compensating refractometer. Measurements taken from the College Station location were done using a hand-held refractometer in which juice from individual fruit was measured and the average of fruits was recorded. This procedure was also used for both years at the Fowler location, but a different method was also used by the Fruit Dynamics staff. They used a composite sample consisting of macerated fruit pulp that was then centrifuged to collect juice from a five fruit sample.. Brix data obtained from the two procedures proved to be highly correlated, thus data from the two samples were averaged for entry.

Titratable acidity was measured manually at both locations based on a five fruit sample. Samples from the Fowler location were stored in a cold room at approximately 4 to 5 °C and evaluated by the Fruit Dynamics staff within two to five days in cold storage after harvest. Juice from the same composite fruit sample used for soluble solids measurement was used for titratable acidity. At the College Station location, fruit were squeezed by hand and the resulting juice stored in 60 mL plastic containers at approximately -20°C. Frozen samples were allowed to thaw at room temperature for approximately two hours prior to their immediate use. For samples from both locations, juice was filtered using a piece of cheese cloth. Ten grams of filtered juice was diluted with 30 mL of de-ionized water and placed in a 40 mL glass beaker. Samples were

titrated with 0.1 N NaOH to pH of 8.1. A two point calibration pH meter was used to determine the titration endpoint. Results were expressed as equivalents of anhydrous malic acid per 1000 millimeters of juice (eq H^+/1000 mL). The following conversion formula was used:

TA = [(ml NaOH x N x 0.067045) ÷ ml juice] x 1000 where,

ml NaOH = ml NaOH used in titration

N = Normality of NaOH

0.067045 = meq weight of malic acid

Pit weight measurements were reported as the average mass from five pits after all flesh had been removed. The majority of all pits from clingstone fruit were removed of most bulk flesh and frozen for later use. Pits were later allowed to thaw at room temperature and immersed in 0.1% laboratory grade Polygalactoranse (a pectin degrading enzyme) for 24 hours to dissolve the remaining flesh from the outer pit surface. Any remaining flesh was removed by scrubbing and rinsing the pits. Pits were allowed to dry before weighing.

3.3.6 Statistical analysis

All statistical analyses were performed using JMP software, Version 9.0, SAS Institute Inc., Cary, NC, 1989 – 2010.

Prior to statistical analyses, data were tested for normality using a Shapiro-Wilcox test. Data from all traits proved to be non-normally distributed. An array of transformations were performed and tested for normality, all of which resulted in the assumption of normality not being met. In addition to testing the effectiveness of each transformation with regard to normality, the model for variance components was also run using the data resulting from each transformation. Output from the analysis model (below) were compared to that of the non-transformed data by evaluating the R^2 value and the genotypic variance component value. In every case, these values were smaller than that of the non-transformed data. Therefore the non-transformed data were used throughout this study.

The additive genetic (σ^2_a), non-additive genetic (σ^2_{di}), environmental (σ^2_e), and genotype x environment (σ^2_{gxe}) variances were estimated using a restricted maximum likelihood (REML) mixed model with all random effects. The variances are reported from the covariance parameter estimate report in JMP. There were three sets of data: Fowler, 2011; Fowler, 2012; College Station, 2012. Year 2012 was found to have differing effects in the CA and TX different locations, so year and location were treated as single environments including: CA-2011, CA-2012, and TX-2012. Parentage (male and female) was also taken into account for all progenies.

Because there was no replication included in the model (only the parents were replicated), there was no residual and all variance was partitioned into one of the following components: σ^2_a (additive genetic); σ^2_{di} (non-additive genetic); (σ^2_e) environmental; σ^2_{gxe} (genotype x environment).

Broad sense heritability estimates were calculated as:

$$H_{bi}^2 = \frac{\hat{\sigma}_G^2}{\hat{\sigma}_G^2 + \frac{\hat{\sigma}_{GE}^2}{e}}$$

Narrow sense heritability estimates were calculated as:

$$h_{bi}^2 = \frac{\hat{\sigma}_A^2}{\hat{\sigma}_G^2 + \frac{\hat{\sigma}_{GE}^2}{e}}$$

Where,

$\hat{\sigma}_A^2$ = estimated additive genetic variance

$\hat{\sigma}_G^2$ = estimated genetic variance

$\hat{\sigma}_{GE}^2$ = estimated genotype x environment variance

e = number of environments

A bivariate model was used to estimate phenotypic correlations. Correlations were computed on a pair-wise basis for all traits. Significance of correlation estimates were discussed based on the magnitude of the estimate because the sampling variances for the correlation estimates were not available (de Souza et al., 1998a). Thus, correlation estimate of ≥0.65 was considered strong to very strong; a correlation estimate

Table 18. Number of observations used in variance component and heritability estimates for nine peach fruit quality traits evaluated for two years at Fowler, CA and for one year at College Station, TX.

Trait	Number of observations
Fruit ground color	711
Flesh color	703
Red in flesh	702
Red around pit	701
Fruit firmness	655
Flesh adherence	700
Soluble solids	687
Titratable acidity	634
Pit weight	530

between 0.50 and 0.64 was considered moderately strong; a correlation estimate between 0.30 and 0.49 were considered moderately weak

3.4 Results and discussion

3.4.1 Variance component and heritability

Variability among progeny was comparable to that of parents ranging from 0 to 2 for ground color (Tables 19 and 20). Fruit ground color was subject to strong genotype x environment interaction that explained approximately 65% of the total phenotypic variance (Table 21). Fruit ground color exhibited moderately high heritability ($h^2 = 0.64$) (Table 21) and genetic improvement of this trait should be possible. Green color in the fruit skin and flesh is undesirable, and a greater understanding of the genetic control for this trait would be very useful.

Modest variability was associated with red in flesh. Variability for red in flesh was slightly higher among progeny (0 to 4 on a zero to ten scale) with a mean of 0.39 (Table 19) than among parents (0 to 2 on a zero to ten scale) (Table 20). This trait appeared to have a strong genotype x environment effect accounting for approximately 56% of the total variance (Table 21). Red in flesh exhibited low narrow-sense heritability ($h^2 = 0.20$) and only moderate broad sense heritability ($H^2 = 0.40$) (Table 21).

Both the means and measures of variability for fruit firmness among progeny were comparable to that of the parents (Tables 19 and 20). Firmness varied widely from a minimum of zero to a maximum of 17.1 among progeny with a mean of 7.61 (Table

Table 19. Descriptive statistics of six peach fruit quality traits evaluated for nine progeny for two years at Fowler, CA and for one year at College Station, TX.

Trait	N	Mean	Phenotypic Variance	Standard Deviation	C.V.	Min	Max
Fruit ground color	711	1.8	0.23	0.45	25.71	0.0	2.0
Red in flesh	702	0.4	0.35	0.58	148.72	0.0	4.0
Fruit firmness	655	7.6	10.45	3.10	29.67	0.0	17.1
Soluble solids	687	11.8	4.61	2.03	17.23	7.2	22.0
Titratable acidity	634	0.7	0.14	0.36	52.94	0.16	2.18
Pit weight	530	6.4	6.52	1.82	28.62	2.6	17.0

N = Number of observations; C.V. = coefficient of variation; Min = minimum value; Max = maximum value.

[w]Fruit ground color expressed as amount of green color based on 0-2 scale (0 = green, 2 no green); red in flesh based on % red overlay of fruit flesh using 0-10 scale (0 = 0% red overlay, 10 = 100% red overlay); fruit firmness as pounds of force; soluble solids in °Brix; titratable acidity in Eq H^+/1000 mL of juice; pit weight in grams.

Table 20. Descriptive statistics of six peach fruit quality traits evaluated for eight parents for two years at Fowler, CA and for one year at College Station, TX.

Trait	N	Mean	Phenotypic Variance	Standard Deviation	C.V.	Min	Max
Fruit ground color	63	1.7	0.25	0.50	29.41	0.00	2.00
Red in flesh	63	0.3	0.24	0.49	175.00	0.00	2.00
Fruit firmness	36	6.3	14.14	3.76	59.87	0.00	12.04
Soluble solids	63	12.3	2.89	1.70	13.84	9.70	17.00
Titratable acidity	36	0.5	0.12	0.34	64.15	0.15	1.32
Pit weight	40	6.4	3.13	1.77	27.66	4.00	13.00

N = Number of observations; C.V. = coefficient of variation; Min = minimum value; Max = maximum value.

[w]Fruit ground color expressed as amount of green color based on 0-2 scale (0 = green, 2 no green); red in flesh based on % red overlay of fruit flesh using 0-10 scale (0 = 0% red overlay, 10 = 100% red overlay; fruit firmness as pounds of force; soluble solids in °Brix; titratable acidity in Eq H^+/1000 mL of juice; pit weight in grams.

Table 21. Variance component, broad sense heritability (H^2), and narrow sense heritability (h^2) for nine progeny for six peach quality traits evaluated for two years at Fowler, CA and for one year at College Station, TX.

Trait[w]	Variances[y]						H^2	h^2
	V_A	V_{DI}	V_G	V_E	V_{GE}	V_P		
Fruit ground color	0.07	0.02	0.09	0.01	0.15	0.23	0.64	0.50
Red in flesh	0.03	0.03	0.06	0.03	0.27	0.35	0.40	0.20
Fruit firmness	1.32	3.25	4.57	0.06	5.82	10.45	0.70	0.20
Soluble solids	0.74	1.71	2.45	0.36	1.81	4.61	0.80	0.24
Titratable acidity	0.01	0.1	0.11	0.00	0.03	0.14	0.92	0.08
Pit weight	0.06	0.75	0.81	4.35	1.36	6.52	0.64	0.05

[y]V_A = additive genetic variance; V_{DI} = non-additive genetic variance; V_G = genetic variance (additive and non-additive); V_E = environmental variance; V_{GxE} = genotype x environmental variance; V_P = phenotypic variance

[w]Fruit ground color expressed as amount of green color based on 0-2 scale (0 = green, 2 no green); red in flesh based on % red overlay of fruit flesh using 0-10 scale (0 = 0% red overlay, 10 = 100% red overlay; fruit firmness as pounds of force; soluble solids in °Brix; titratable acidity in Eq H^+/1000 mL of juice; pit weight in grams.

Table 22. Comparison of six peach fruit quality traits evaluated for nine progeny in three environments.

	Fowler, CA 2011		Fowler, CA 2012		College Station, TX 2012	
Trait[w]	Mean	Min-Max	Mean	Min/Max	Mean	Min/Max
Fruit ground color	1.9	0.0-2.0	1.7	0.0-2.0	1.7	0.0-2.0
Red in flesh	0.5	0.0-3.0	0.2	0.0-3.0	0.6	0.0-4.0
Fruit firmness	7.4	1.5-15.2	7.9	0.0-17.1	7.2	0.0-15.6
Soluble solids	11.7	7.2-20.8	11.6	7.6-22.0	12.5	8.0-18.5
Titratable acidity	0.7	0.2-1.8	0.7	0.2-2.1	0.6	0.2-1.1
Pit weight	8.7	3.0-17.0	6.3	2.6-11.0	5.1	3.0-8.5

[w]Fruit ground color expressed as amount of green color based on 0-2 scale (0 = green, 2 no green); fruit flesh color expressed as amount of green color based on 0-2 scale (0 = green, 2 = no green); red in flesh based on % red overlay of fruit flesh using 0-10 scale (0 = 0% red overlay, 10 = 100% red overlay); soluble solids in °Brix; titratable acidity in Eq H^+/1000 mL of juice; pit weight in grams.

19). Firmness was also subject to genotype x environment effect explaining approximately 56% of the total variance for this trait (Table 21). It is important to remember that peach is a climacteric fruit and firmness is highly subject to the subjective procedure for determining maturity as well as how quickly the trait was measured following harvest. Heritability for fruit firmness was low ($h^2 = 0.20$) (Table 21), but still higher than the previous report of 0.13 by Hansche et al. (1972). Broad sense heritability for firmness was high ($H^2 = 0.70$), suggesting an important non additive genetic component for this trait. Nevertheless, the moderate amount of variability should allow for genetic improvement of this trait.

The range for soluble solids varied widely from 7.2 to 21.8 °Brix (Table 19). Greater variability was observed among progeny than parents, as reflected by the wider range among progeny (Tables 19 and 20). Genotype x environment interaction contributed to approximately 39% of total variance for soluble solids (Table 21). The low narrow sense heritability estimate of 0.24 (Table 21) for SSC was higher than that of 0.01 reported by Hansche et al. (1972), but was considerably lower than most estimates ($h^2 = 0.33$; 0.43; 0.72) (de Souza et al., 1998b; Monet and Bastard, 1982; Brooks et al., 1993). Broad sense heritability was much higher ($H^2 = 0.80$) (Table 21) supporting the conclusion that sugar content in peach is affected by major genes (Quilot-Turion and Gernard, 2009; Dirlewanger et al., 2009; Cantin et al., 2009). Distribution of soluble solids appeared to be skewed toward the lower end (Appendix 18) suggesting dominance for low sugar in these populations. Nevertheless, some genetic improvement for this trait should be possible, given the observation of transgressive segregation in some progenies,

especially if these genes that appear to be dominant for low SSC can easily be selected against.

A substantial amount of variability was associated with titratable acidity (TA) as indicated by the range (0.16 to 2.18 ml Eq H^+/1000 mL of juice) with a mean of 0.68 (Table 19). Both the range and variance among progeny were comparable to that of the parents for this trait (Tables 19 and 20). Both environmental and genotype x environment effects were minimal for acidity and the non-additive genetic effect was responsible for approximately 71% of the total variance for this trait (Table 21). TA showed very low additive inheritance (h^2 = 0.08) (Table 21), which was lower than the previous low (≤0.19) (Hansche et al., 1986; Hansche and Beres, 1980; Hansche et al., 1972) to moderate (h^2 = 0.31) (de Souza et al., 1998b) estimates. The estimate for broad sense heritability was high (H^2 = 0.92) (Table 21) reflecting the fact that these populations were segregating for the D gene which conditions a low level of acidity (Boudheri et al. 2009 and Dirlewanger et al., 1999). Existence of this major gene in these populations is evident in the bimodal distribution associated with this trait (Appendix 19). Selection for low acid genotypes is relatively easy, given the effect of the major dominant gene for low acidity. Selection for high acid fruit would also be possible by selecting against low acid genotypes.

The range for pit weight varied from 2.6 to 17.0 grams, and transgressive segregation was observed in several progenies. (Tables 19 and 20). Environmental effects accounted for approximately 67% of the total variance (Table 21) as reflected in the comparison that pit weight averaged approximately 72% and 24% greater at Fowler

in 2011 and 2012 than at College Station in 2012 (Table 22). Pit weight exhibited high broad sense heritability (H^2 = 0.64) (Table 21). Non-additive genetic component accounted for 92% of the genetic variance, supporting earlier conclusions that this trait, which has traditionally been considered quantitative, might be controlled by several major genes (Hesse, 1975) although the negatively skewed distribution of pit weight in these populations suggests dominance for small pit size (Appendix 20) rather than for large pits as suggested by Bassi et al. (1989).

3.4.2 Genotype by environment interactions

As mentioned earlier, several traits were affected by a strong genotype x environment (GxE) interaction. GxE interaction has been described as the differential response of genotypes to the environment in which they are grown (Bernardo, 2010). If such interactions exist in the case of specific genotypes across specific environments, selection on the basis of performance for a given trait cannot be practiced in one environment if the plant is expected to perform the same in another (Allard and Bradshaw, 1964). A stability analysis plotting progeny means across environments was generated to make this comparison easier (Appendix 13 through 16).

Fruit ground color was strongly affected by genotype x environment interaction that was responsible for approximately 65% of the total phenotypic variance (Table 21). On a mean basis, ground color was slightly higher at Fowler in 2011 than at Fowler in 2012. Ground color at College Station in 2012 was intermediate between the two Fowler environments (Table 22). This interaction appears to be the result of most families

observed generally not closely following this trend, with three families in particular, unrelated with respect to parentage, deviating severely from this overall trend (Appendix 13).

Red in flesh was also subject to strong genotype x environment effect accounting for approximately 56% of the total variance (Table 21). Red in flesh had an average value of 0.50 at Fowler in 2011 and was much lower at Fowler in 2012, with an average value of 0.23. The highest average value of for this trait was 0.59 at College Station in 2012 (Table 22). The primary source of interaction appeared to be three families, all of which shared one common parent in Y434-40, that severely deviated from this trend (Appendix 14).

Fruit firmness was strongly affected by genotype x environment interaction, which explained approximately 56% of the total variance for this trait. Average firmness was slightly higher the second year at Fowler (Table 22) with most families more or less adhering to this trend with little interaction (Appendix 15). Average firmness was slightly lower at College Station in 2012 than at Fowler in 2012 (Table 22). Much of the interaction appears to result from the erratic behavior among families between all three environments (Appendix 15). This behavior may be largely an effect of poor sampling, as there was no clear explanation for these interactions with respect to parentage. Fruit at the College Station site were not always harvested following as carefully and timely as at the Fowler site. As mentioned earlier, peach is a climacteric fruit, thus assessment of firmness is highly dependent on the precise sampling and timely measurement of this trait.

Soluble solids was also strongly affected by genotype x environment response that accounted for approximately 39% of total variance for this trait. Average soluble solids concentration was generally stable as a whole and with respect to performance of individual families across the Fowler environments as might be expected given the greater seasonable stability from year to year at this location (Appendix 16). Soluble solids at College Station in 2012 were on average approximately 7% and 8% higher than at Fowler in 2011 and 2012 (Table 22) likely due to greater environmental stresses afflicting this site such as shallow soils as well as smaller fruit size observed at this site (Table 9 in Chapter II)- all of which can result in higher soluble solids in peach (Veihmeyer and Hendrickson, 1949). Most of the genotype environment interaction appeared to result from deviation from this general trend by families splitting into two groups. Approximately half of the families, most of which shared 'Victor' as a parent, performed more favorably, while the other group, most of which were derived from the parent TX2B136, performed less favorably at College Station in 2012 relative to Fowler in 2012 (Appendix 16). On average, both of these groups of families had similar fruit development periods.

3.4.3 Major gene effects on heritability

Two major genes- pantao and nectarine can have strong pleiotropic effects on several traits related to fruit quality in peach, with nectarines tending to have greater firmness, soluble solids, and acidity, while pantao fruit typically have higher soluble solids, but lower firmness and acidity (Wang, 2009; Wang et al., 2010; Wen et al.,

1995a&b; Wu, 2003a&b). Nectarine is inherited as a single recessive gene and produces fruit without pubescence (Blake, 1932). Pantao is inherited as a single dominant trait producing flattened or saucer-shape fruit (Scorza and Sherman, 1996). Because several of these progenies were segregating for one or both of these traits, the analysis was run without pantao, nectarine, or both types of seedlings to assess their influence on the heritability for these traits. Approximately 15% fewer data points were observed with the exclusion of nectarine, and approximately 7% fewer without pantao seedlings.

Additive inheritance for soluble solids was lower when nectarine genotypes were excluded from the analysis ($h^2 = 0.13$) (Table 23). Nectarines tend to have higher SSC compared to peaches (Cantin et al., 2009; Wang et al., 2010; Wen et al., 1995); therefore, removal of these higher sugar individuals resulted in the 78% lower additive variance when nectarines were removed (Table 23). Nectarine seedlings were on average 2.04 °Brix or approximately 17% higher than peach seedlings among progenies segregating for this trait.

Heritability of titratable acidity, estimated as narrow sense, was reduced to zero with the exclusion of nectarine alone and both pantao and nectarine genotypes from the analysis for titratable acidity (TA), and resulted from the rounded additive genetic variance being reduced to zero for these datasets (Table 23). Although the resulting loss of heritability was appreciable, the original estimate ($h^2 = 0.08$) was already extremely low resulting in the same conclusion on heritability for this trait.

Table 23. Variance component, broad sense heritability (H^2), and narrow sense heritability (h^2) for soluble solids and titratable acidity evaluated for two years at Fowler, CA and for one year at College Station, TX comparing the effect of the removal of nectarine, pantao, and both types of seedlings.

Trait[w]	Variances[y]						H^2	h^2
	V_A	V_{DI}	V_G	V_E	V_{GxE}	V_P		
Soluble solids	0.74	1.71	2.45	0.36	1.81	4.61	0.80	0.24
Soluble solids[p]	0.50	1.19	1.69	0.37	1.79	3.85	0.74	0.22
Soluble solids[n]	0.21	0.95	1.16	0.70	1.35	3.20	0.72	0.13
Soluble solids[pn]	0.12	0.81	0.93	0.72	1.38	3.04	0.67	0.09
Titratable acidity	0.01	0.10	0.11	0.00	0.03	0.14	0.92	0.08
Titratable acidity[p]	0.01	0.09	0.10	0.00	0.03	0.13	0.91	0.09
Titratable acidity[n]	0.00	0.07	0.07	0.00	0.02	0.10	0.91	0.00
Titratable acidity[pn]	0.00	0.07	0.07	0.00	0.02	0.10	0.91	0.00

[y]V_A = additive genetic variance; V_{DI} = non-additive genetic variance; V_G = genetic variance (additive and non-additive); V_E = environmental variance; V_{GxE} = genotype x environmental variance; V_P = phenotypic variance.

[w]Soluble solids in °Brix; titratable acidity in Eq H^+/1000 mL of juice.

[p]Analysis run without pantao seedlings.

[n]Analysis run without nectarine seedlings.

[pn]Analysis run without both pantao and nectarine seedlings.

3.4.4 Phenotypic correlations

Phenotypic correlations are an estimate of the relationship between the two traits based on both environmental and genetic factors, limiting their application (de Souza et al., 1998b). Also, when heritability for a given trait is low, phenotypic correlation is primarily a function of environmental correlation (Falconer, 1989). The ultimate application for inter-trait correlation in plant breeding is indirect selection (Searle, 1965). Significance of correlation estimates were discussed based on the magnitude of the estimate because the sampling variances for the correlation estimates were not available (de Souza et al., 1998b). Thus, a correlation estimate of ≥0.65 was considered strong to very strong; a correlation estimate between 0.50 and 0.64 was considered moderately strong; a correlation estimate between 0.30 and 0.49 was considered moderately weak.

Correlations of fruit firmness and soluble solids with date of ripening (r = 0.38; 0.32) and FDP (r = 0.39; 0.33) (Table 24) were moderately weak. The correlations between soluble solids and both ripening date and FDP (Table 24) support earlier conclusions that it is more difficult to select for high sugar progeny that are earlier ripening or have a short development period (de Souza et al., 1998b; Wu, 2003).

Pit weight showed moderately weak correlations with FDP (r = 0.33), fruit weight (r = 0.51), and fruit diameter (r = 0.38) (Table 24). The relationship correlation of fruit diameter and pit weight was stronger (r = 0.49) (Appendix 4) when pantao seedlings were removed from the analysis, which tend have smaller pits. This is to be expected given the positive relationships between pit weight and fruit size (Chalmers

Table 24. Phenotypic correlations among 14 peach tree and fruit quality traits for two years at Fowler, CA and one year at College Station, TX.[z]

Characters[y]	Firmness	S.S.	T.A.	Pit weight
Bloom	-0.01	0.02	-0.19	-0.21
Ripe	0.38	0.32	-0.02	0.26
FDP	0.39	0.33	0.04	0.33
Pubescence	-0.11	-0.44	-0.31	0.02
Blush	-0.20	-0.15	-0.09	-0.08
Weight	0.19	-0.12	-0.14	0.51
Diameter	0.25	-0.03	-0.10	0.38
Tip	0.00	0.15	0.13	0.09
Shape	-0.14	0.15	0.06	0.06

[z]Correlation values $r_p \geq 0.65$; $0.64 \geq r_p \geq 0.50$; $0.49 \geq r_p \geq 0.30$; $r_p < 0.30$ were considered strong or very strong, moderately strong, moderately weak, and weak or very weak, respectfully. Correlation values ≥ are underlined.

[y]Date of full bloom and date of ripening expressed in Julian Days; fruit development period in days; fruit pubescence visually based on 0-9 scale (0 = no pubescence, 6 or higher = greater pubescence than modern cultivars); fruit red blush visually based on % coverage of red blush on skin using 0-5 scale (0 = 0% red coverage, 1 = 1%-20%, 2 = 21%-50%, 3 = 51%-80%, 4 = 81%-99%, 5 = 100%); fruit weight in grams; fruit diameter in millimeters; fruit tip visually based on 0-9 scale (6 or lower = very prominent fruit tip, 9 = completely oblate fruit tip); fruit shape visually based on 0-9 scale (6 or lower = large suture bulge and prominent tip, 9 = no pronounced suture and oblate tip; S.S. = soluble solids in °Brix; T.A. = titratable acidity in Eq H^+/1000 mL of juice; pit weight in grams.

and van den Ende, 1975), and fruit size with FDP (Chapter II). The correlation between pit weight and FDP was higher (r = 0.39) (Appendix 4) when the smaller pit pantao genotypes were removed from the analysis.

Pubescence with soluble solids and titratable acidity showed moderately weak negative correlations (r = -0.44; -0.31) (Table 24). As expected, these values were reduced substantially (r = -0.16; -0.09) (Appendix 5) when nectarines were removed from the analysis. Nectarines tend to have higher SSC and greater acidity than peaches (Cantin et al., 2009; Wang, 2009; Wang et al., 2010; Wen et al., 1995) in both segregating progenies and germplasm collections.

3.5 Conclusions

A large amount of variability was associated with all traits, except for fruit ground color and red in flesh, which exhibited low to moderate variability. Variability is a major component in the estimation of heritability, and both are necessary for genetic improvement. Although most traits had low narrow sense heritability, genetic improvement of these traits should be possible, given their appreciable phenotypic variability and high broad sense heritability. Slower progress should be expected for red in flesh, given its smaller variability and genetic variance components. Heritability and genetic correlations are dependent on the specific germplasm and environments used in each investigation and the results of this study differ from some previous studies.

Only one trait, fruit ground color, showed moderate to high narrow sense heritability (h^2 = 0.50). All other traits (red in flesh, fruit firmness, soluble solids, TA,

and pit weight) showed low additive inheritance as earlier reported, but had moderate to high broad sense heritability suggesting an important non additive genetic component for these traits. Broad sense estimate values ranged from 0.40 for red in flesh to 0.92 for acidity. Existence of dominance for small pit weight (contrary to a previous report) and low soluble solids was also suggested in these populations.

Most traits were not strongly influenced by the environment; however, pit weight showed major differences between sites. Pit size, similar to fruit size, was consistently larger at Fowler than at College Station.

Most traits were subject to genotype x environment effects, suggesting that, for these traits, selection should only be practiced where the plants are meant to be grown. All but two traits (TA and pit weight) showed differential response with respect to genotype across different environments. For fruit ground color, fruit firmness, and soluble solids the interaction appeared to be the result of most families behaving differently from the general trend across environments, while only two families appeared to deviate from the trend for red in flesh.

Several progenies were segregating for two major genes, pantao and nectarine, which are reported to have a strong pleiotropic effects on fruit firmness, soluble solids, TA , and pit weight, thus the analysis was run without pantao, nectarine, and both types of seedlings. Removal of nectarine seedlings from the analysis resulted in a lower narrow sense estimate of heritability for soluble solids. Lower narrow sense heritability was associated with TA when pantao and pantao and nectarine seedlings were removed. The exclusion of nectarine and pantao seedlings from the analysis resulted in

approximately 15% and 7% fewer data points for these traits. Overall, heritability was not strongly affected by these major genes in terms of low or moderate heritability classifications.

The ultimate implication of high correlations between traits is the ability to practice indirect selection. The usefulness of phenotypic correlations would be limited when heritability is low for both related traits because these correlations are based on the relationships between traits based on both genetic and environmental factors. None of the correlations discussed were strong enough, given the relatively low heritability among related traits, to be considered as useful for indirect selection.

CHAPTER IV

CONCLUSION

Most traits evaluated were associated with large phenotypic variability, while fruit tip and fruit shape exhibited more moderate measures of variability. Red in the flesh showed low to moderate variability. Variability is a major component in the estimation of heritability, and both are necessary for genetic improvement. The date of full bloom was highly heritable, whereas slightly less than half of the traits were estimated to be moderately heritable, and slightly more than half showed low and one showed high additive inheritance. Given the appreciable variability and moderate heritability, some genetic advance should be possible for most traits evaluated. Heritability and genetic correlations are dependent on the specific germplasm and environments used in each investigation and the results of this study differ from some previous studies.

Date of full bloom and fruit ground color were highly and moderately heritable (h^2 = 0.62, h^2 = 0.50) on a narrow sense basis, whereas date of ripening and fruit development period (FDP) were associated with low heritability in spite of being widely reported as highly heritable traits. Several other traits (red in flesh, fruit firmness, soluble solids, TA, and pit weight) showed low additive inheritance as earlier reported. Broad sense estimates for all of these lowly heritable (h^2) traits were moderate to high, suggesting an important non additive genetic component. Contrary to previous studies, fruit weight showed low additive inheritance, although the broad sense heritability was high for this trait. Distribution of fruit weight, pit weight, and soluble solids was

negatively skewed, suggesting dominance for small fruit and pit size and low soluble solids. Moderate narrow sense heritability was associated with all the other traits (fruit pubescence, fruit red blush, fruit pubescence, fruit diameter, fruit tip, and fruit shape) as expected from previous studies. Heritability ranged from 0.38 for fruit shape to 0.46 for fruit red blush.

Several traits were strongly influenced by the environment (date of full bloom, date of ripening, and FDP) mainly in response to temperature differences between sites, as trees typically bloomed earlier and fruit ripened later at Fowler than at College Station. Pit weight was consistently larger at Fowler than at College Station.

Several traits were subject to strong genotype x environment effects, suggesting that, for these traits, selection should only be practiced where the plants are meant to be grown. Fruit red blush, fruit weight, fruit diameter, fruit tip, fruit shape, and red in flesh showed differential response with respect to genotype across different environments and, for these traits, the interaction appeared to be the result of one or two progeny families behaving differently from the general trend across environments. Several other traits were also influenced by this effect. For fruit ground color, fruit firmness, and soluble solids the interaction appeared to be the result of most families behaving differently from the general trend across environments.

Several progenies were segregating for two major genes, pantao and nectarine, which have been reported to have pleiotropic effects on fruit size, fruit red blush, and fruit shape; thus, the analysis was run without pantao, nectarine, and both types of seedlings for these traits. Removal of nectarine seedlings from the analysis resulted in

lower heritability estimates for fruit pubescence, fruit red blush, fruit weight, and fruit tip, and soluble solids. Heritability for fruit weight was higher with the removal of pantao seedlings, while fruit diameter showed a lower value when both pantao and nectarine were removed. Additive heritability was lower when nectarine, and both pantao types of seedlings were removed. The exclusion of nectarine and pantao seedlings from the analysis resulted in approximately 15% and 7% fewer data points for these traits. Overall, heritability was not strongly affected by these major genes, except in the case of fruit pubescence, which went from moderate to low heritability (h^2) with the exclusion of nectarine seedlings as well as fruit diameter, which had the same response with the removal of both pantao and nectarine seedlings from the analysis.

The ultimate implication of high correlations between traits is in the ability to practice indirect selection. Because phenotypic correlations are based on the relationships between traits, as influenced by both genetic and environmental factors, their usefulness would be limited, especially when heritability is low for both related traits. None of the correlations were strong enough among traits to allow for indirect selection, as most relationships were the result of environmental or physiological relationships, or were simply different measures of the same trait.

Date of ripening and FDP were strongly correlated (r = 0.94), suggesting that ripening date is a reliable estimator of FDP. The negative correlation between date of full bloom and FDP (r = -0.45) suggests that earlier blooming during cool temperatures tends to extend the fruit development period. The moderately weak negative correlations of fruit red blush with date of ripening (r = -0.31) and FDP (-0.38) were most likely a

function of decreased blush caused by lower light exposure to fruit due to denser tree canopy later in the season. Date of full bloom and fruit tip were moderately and negatively correlated (r = -0.40) as reported previously, as earlier blooming seedlings tend to produce rounder tip fruit in response to cooler temperatures during bloom and early development.

Fruit weight and fruit diameter were moderately strongly correlated with date of ripening (r = 0.54; 0.55) and FDP (r = 0.50; 0.51) respectively. As previously reported, fruit size tends to increase when fruit ripens later as a result of greater resources available for growth.

Fruit weight and fruit diameter were strongly correlated (r = 0.83) as expected, suggesting that both are reliable measures of fruit size. Fruit tip and fruit shape were moderately weakly correlated (r = 0.36), which was not surprising considering that over all fruit shape is partially a representation of fruit tip, and was weaker without rounder tip nectarines and stronger without pantao, which received high tip ratings, but often lower ratings for fruit shape based on irregular sutures.

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APPENDIX A

A-1. Phenotypic correlations among nine peach tree and fruit quality traits for two years at Fowler, CA and one year at College Station, TX. with pantao genotypes removed.[z]

Traits[y]	Bloom	Ripe	FDP	Pub.	Blush	Weight	Diam.	Tip	Shape
Bloom	---	-0.15	-0.45	0.32	0.03	-0.11	-0.06	-0.41	-0.26
Ripe	-0.15	---	0.94	0.09	-0.32	0.57	0.53	0.02	0.04
FDP	-0.45	0.94	---	-0.01	-0.39	0.53	0.50	0.12	0.08
Pubesc.	0.32	0.09	-0.01	---	-0.06	0.26	0.22	-0.30	-0.24
Blush	0.03	-0.32	-0.39	-0.06	---	-0.28	-0.24	0.11	0.18
Weight	-0.11	0.57	0.53	0.26	-0.28	---	0.90	0.00	0.06
Diam.	-0.06	0.53	0.50	0.22	-0.24	0.90	---	0.03	0.06
Tip	-0.41	0.02	0.12	-0.30	0.11	0.00	0.03	---	0.41
Shape	-0.26	0.04	0.08	-0.24	0.18	0.06	0.06	0.41	---

[z]Correlation values $r_p \geq 0.65$; $0.64 \geq r_p \geq 0.50$; $0.49 \geq r_p \geq 0.30$; $r_p < 0.30$ were considered strong or very strong, moderately strong, moderately weak, and weak or very weak, respectfully. Correlation values ≥ are underlined.

[y]Date of full bloom and date of ripening expressed in Julian Days; fruit development period in days; fruit pubescence visually based on 0-9 scale (0 = no pubescence, 6 or higher = greater pubescence than modern cultivars); fruit red blush visually based on % coverage of red blush on skin using 0-5 scale (0 = 0% red coverage, 1 = 1%-20%, 2 = 21%-50%, 3 = 51%-80%, 4 = 81%-99%, 5 = 100%); fruit weight in grams; fruit diameter in millimeters; fruit tip visually based on 0-9 scale (6 or lower = very prominent fruit tip, 9 = completely oblate fruit tip); fruit shape visually based on 0-9 scale (6 or lower = large suture bulge and prominent tip, 9 = no pronounced suture and oblate tip.

A-2. Phenotypic correlations among nine peach tree and fruit quality traits for two years at Fowler, CA and one year at College Station, TX. with nectarine genotypes removed.[z]

Traits[y]	Bloom	Ripe	FDP	Pub.	Blush	Weight	Diam.	Tip	Shape
Bloom	---	-0.21	-0.50	0.08	0.17	-0.21	-0.20	-0.33	-0.17
Ripe	-0.21	---	0.94	0.06	-0.28	0.55	0.54	0.09	0.08
FDP	-0.50	0.94	---	0.03	-0.40	0.53	0.55	0.17	0.09
Pubesc.	0.08	0.06	0.03	---	0.21	0.02	-0.05	0.06	-0.04
Blush	0.17	-0.28	-0.40	0.21	---	-0.21	-0.20	-0.01	0.18
Weight	-0.21	0.55	0.53	0.02	-0.21	---	0.84	0.09	0.17
Diam.	-0.20	0.54	0.55	-0.05	-0.20	0.84	---	0.28	0.19
Tip	-0.33	0.09	0.17	0.06	-0.01	0.09	0.28	---	0.31
Shape	-0.17	0.08	0.09	-0.04	0.18	0.17	0.19	0.31	---

[z]Correlation values $r_p \geq 0.65$; $0.64 \geq r_p \geq 0.50$; $0.49 \geq r_p \geq 0.30$; $r_p < 0.30$ were considered strong or very strong, moderately strong, moderately weak, and weak or very weak, respectfully. Correlation values ≥ are underlined.

[y]Date of full bloom and date of ripening expressed in Julian Days; fruit development period in days; fruit pubescence visually based on 0-9 scale (0 = no pubescence, 6 or higher = greater pubescence than modern cultivars); fruit red blush visually based on % coverage of red blush on skin using 0-5 scale (0 = 0% red coverage, 1 = 1%-20%, 2 = 21%-50%, 3 = 51%-80%, 4 = 81%-99%, 5 = 100%); fruit weight in grams; fruit diameter in millimeters; fruit tip visually based on 0-9 scale (6 or lower = very prominent fruit tip, 9 = completely oblate fruit tip); fruit shape visually based on 0-9 scale (6 or lower = large suture bulge and prominent tip, 9 = no pronounced suture and oblate tip.

A-3. Phenotypic correlations among nine peach tree and fruit quality traits for two years at Fowler, CA and one year at College Station, TX. with pantao and nectarine genotypes removed.[z]

Traits[y]	Bloom	Ripe	FDP	Pub.	Blush	Weight	Diam.	Tip	Shape
Bloom	---	-0.20	-0.49	0.08	0.17	-0.23	-0.19	-0.32	-0.18
Ripe	-0.20	---	0.94	0.06	-0.29	0.58	0.55	0.07	0.08
FDP	-0.49	0.94	---	0.03	-0.41	0.57	0.56	0.13	0.09
Pubesc.	0.08	0.06	0.03	---	0.21	0.02	-0.06	0.07	-0.05
Blush	0.17	-0.29	-0.41	0.21	---	-0.24	-0.20	0.05	0.18
Weight	-0.23	0.58	0.57	0.02	-0.24	---	0.91	0.15	0.18
Diameter	-0.19	0.55	0.56	-0.06	-0.20	0.91	---	0.19	0.18
Tip	-0.32	0.07	0.13	0.07	0.05	0.15	0.19	---	0.35
Shape	-0.18	0.08	0.09	-0.05	0.18	0.18	0.18	0.35	---

[z]Correlation values $r_p \geq 0.65$; $0.64 \geq r_p \geq 0.50$; $0.49 \geq r_p \geq 0.30$; $r_p < 0.30$ were considered strong or very strong, moderately strong, moderately weak, and weak or very weak, respectfully. Correlation values ≥ are underlined.

[y]Date of full bloom and date of ripening expressed in Julian Days; fruit development period in days; fruit pubescence visually based on 0-9 scale (0 = no pubescence, 6 or higher = greater pubescence than modern cultivars); fruit red blush visually based on % coverage of red blush on skin using 0-5 scale (0 = 0% red coverage, 1 = 1%-20%, 2 = 21%-50%, 3 = 51%-80%, 4 = 81%-99%, 5 = 100%); fruit weight in grams; fruit diameter in millimeters; fruit tip visually based on 0-9 scale (6 or lower = very prominent fruit tip, 9 = completely oblate fruit tip); fruit shape visually based on 0-9 scale (6 or lower = large suture bulge and prominent tip, 9 = no pronounced suture and oblate tip.

A-4. Phenotypic correlations among 14 peach tree and fruit quality traits evaluated nine progeny for two years at Fowler, CA and one year at College Station, TX with pantao genotypes removed.[z]

Characters[y]	Firmness	S.S.	T.A.	Pit weight
Bloom	0.00	0.05	-0.19	-0.24
Ripe	0.38	0.31	-0.03	0.31
FDP	0.38	0.31	0.03	0.39
Pubescence	-0.12	-0.43	-0.31	0.03
Blush	-0.20	-0.12	-0.06	-0.13
Weight	0.23	-0.10	-0.11	0.51
Diameter	0.22	-0.10	-0.11	0.49
Tip	-0.08	0.08	0.10	0.19
Shape	-0.13	0.16	0.09	0.07

[z]Correlation values $r_p \geq 0.65$; $0.64 \geq r_p \geq 0.50$; $0.49 \geq r_p \geq 0.30$; $r_p < 0.30$ were considered strong or very strong, moderately strong, moderately weak, and weak or very weak, respectfully. Correlation values ≥ are underlined.

[y]Date of full bloom and date of ripening expressed in Julian Days; fruit development period in days; fruit pubescence visually based on 0-9 scale (0 = no pubescence, 6 or higher = greater pubescence than modern cultivars); fruit red blush visually based on % coverage of red blush on skin using 0-5 scale (0 = 0% red coverage, 1 = 1%-20%, 2 = 21%-50%, 3 = 51%-80%, 4 = 81%-99%, 5 = 100%); fruit weight in grams; fruit diameter in millimeters; fruit tip visually based on 0-9 scale (6 or lower = very prominent fruit tip, 9 = completely oblate fruit tip); fruit shape visually based on 0-9 scale (6 or lower = large suture bulge and prominent tip, 9 = no pronounced suture and oblate tip; S.S. = soluble solids in °Brix; T.A. = titratable acidity in Eq H^+/1000 mL of juice; pit weight in grams.

A-5. Phenotypic correlations among 14 peach tree and fruit quality traits evaluated for nine progeny for two years at Fowler, CA and one year at College Station, TX with nectarine genotypes removed.[z]

Characters[y]	Firmness	S.S.	T.A.	Pit weight
Bloom	-0.01	0.20	-0.14	-0.24
Ripe	0.38	0.37	-0.04	0.24
FDP	0.38	0.32	0.01	0.31
Pubescence	-0.14	-0.16	-0.09	0.12
Blush	-0.24	-0.14	-0.12	-0.07
Weight	0.19	0.00	-0.05	0.55
Diameter	0.26	0.11	0.00	0.39
Tip	-0.02	-0.05	0.05	0.11
Shape	-0.14	0.07	0.01	0.05

[z]Correlation values $r_p \geq 0.65$; $0.64 \geq r_p \geq 0.50$; $0.49 \geq r_p \geq 0.30$; $r_p < 0.30$ were considered strong or very strong, moderately strong, moderately weak, and weak or very weak, respectfully. Correlation values ≥ are underlined.

[y]Date of full bloom and date of ripening expressed in Julian Days; fruit development period in days; fruit pubescence visually based on 0-9 scale (0 = no pubescence, 6 or higher = greater pubescence than modern cultivars); fruit red blush visually based on % coverage of red blush on skin using 0-5 scale (0 = 0% red coverage, 1 = 1%-20%, 2 = 21%-50%, 3 = 51%-80%, 4 = 81%-99%, 5 = 100%); fruit weight in grams; fruit diameter in millimeters; fruit tip visually based on 0-9 scale (6 or lower = very prominent fruit tip, 9 = completely oblate fruit tip); fruit shape visually based on 0-9 scale (6 or lower = large suture bulge and prominent tip, 9 = no pronounced suture and oblate tip; S.S. = soluble solids in °Brix; T.A. = titratable acidity in Eq H^+/1000 mL of juice; pit weight in grams.

A-6. Phenotypic correlations among 14 peach tree and fruit quality traits evaluated for nine progeny for two years at Fowler, CA and one year at College Station, TX with pantao and nectarine genotypes removed.[z]

Characters[y]	Firmness	S.S.	T.A.	Pit weight
Bloom	0.02	0.24	-0.13	-0.28
Ripe	**0.38**	**0.36**	-0.05	0.28
FDP	**0.38**	**0.30**	0.00	**0.37**
Pubescence	-0.15	-0.17	-0.08	0.14
Blush	-0.23	-0.13	-0.10	-0.11
Weight	0.24	0.01	-0.03	**0.54**
Diameter	0.23	0.04	-0.01	**0.50**
Tip	-0.13	-0.14	0.01	0.23
Shape	-0.13	0.04	0.02	0.08

[z]Correlation values $r_p \geq 0.65$; $0.64 \geq r_p \geq 0.50$; $0.49\ r_p \geq 0.30$; $r_p < 0.30$ were considered strong or very strong, moderately strong, moderately weak, and weak or very weak, respectfully. Correlation values ≥ are underlined.

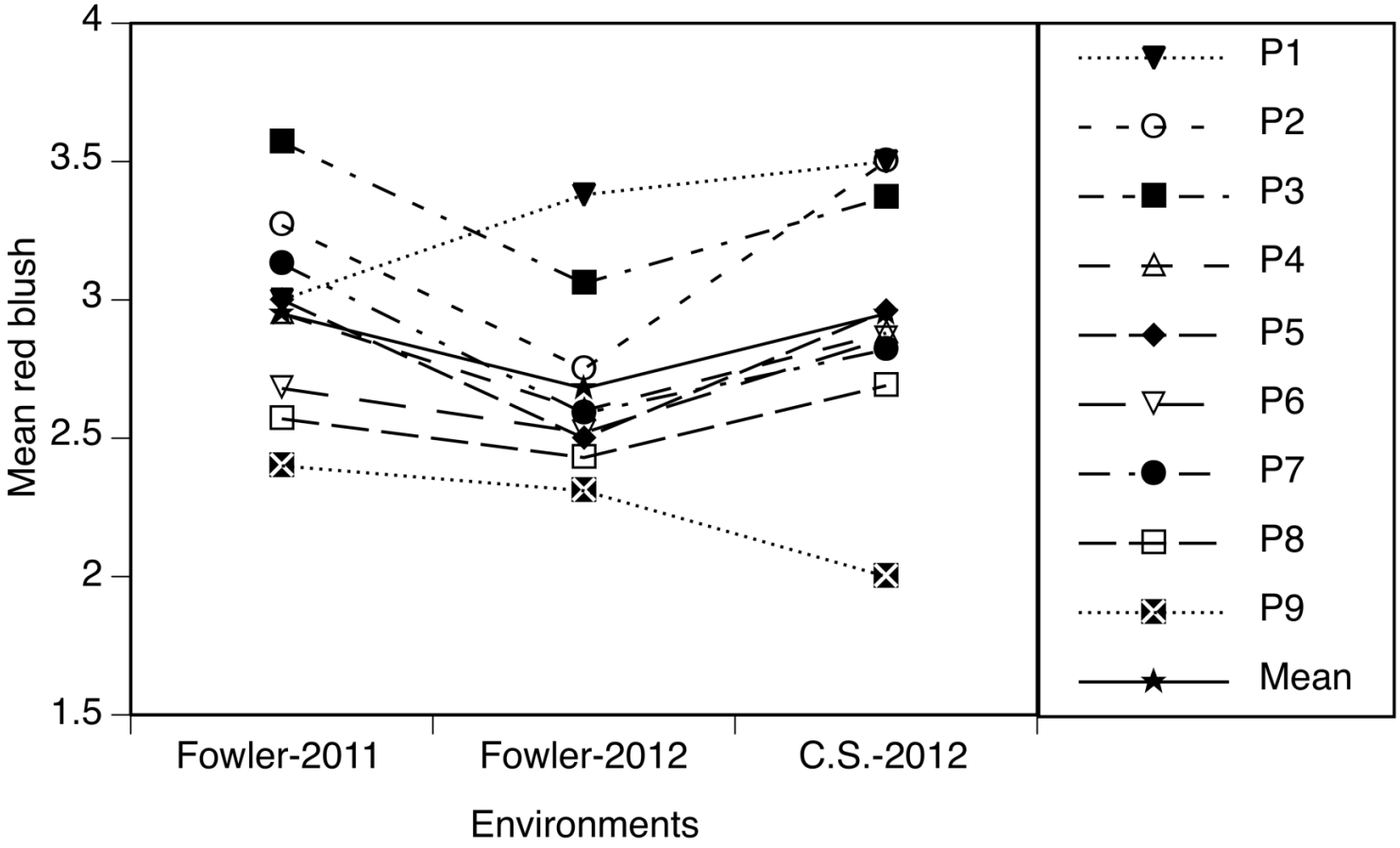
[y]Date of full bloom and date of ripening expressed in Julian Days; fruit development period in days; fruit pubescence visually based on 0-9 scale (0 = no pubescence, 6 or higher = greater pubescence than modern cultivars); fruit red blush visually based on % coverage of red blush on skin using 0-5 scale (0 = 0% red coverage, 1 = 1%-20%, 2 = 21%-50%, 3 = 51%-80%, 4 = 81%-99%, 5 = 100%); fruit weight in grams; fruit diameter in millimeters; fruit tip visually based on 0-9 scale (6 or lower = very prominent fruit tip, 9 = completely oblate fruit tip); fruit shape visually based on 0-9 scale (6 or lower = large suture bulge and prominent tip, 9 = no pronounced suture and oblate tip; S.S. = soluble solids in °Brix; T.A. = titratable acidity in Eq H^+/1000 mL of juice; pit weight in grams.

A-7. Minimum, average mean, and maximum temperatures (°C) by month for three environments.

Months	Fowler, CA - 2011			Fowler, CA - 2012			College Station, TX - 2012		
	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max
November[y]	-0.6	12.2	32.2	3.3	12.2	24.4	0.0	17.2	30.6
December[y]	-1.1	10.6	19.4	-2.2	7.8	20.6	-3.3	11.7	25.0
January	0.6	8.3	17.2	-2.2	10.0	20.0	-2.2	13.3	26.1
February	-1.1	10.0	23.9	2.2	11.7	25.0	-0.6	14.4	31.1
March	2.2	13.3	27.2	1.7	13.3	25.6	3.3	19.4	29.4
April	2.8	16.1	30.0	3.3	17.2	35.6	10.0	22.8	32.8
May	7.8	18.9	35.6	9.4	22.2	37.2	16.1	26.1	34.4
June	9.4	23.9	41.7	11.1	25.6	42.8	20.0	29.4	41.1
July	13.9	27.8	41.1	15.6	28.9	42.2	22.2	29.4	38.3
August	16.1	28.3	40.0	15.6	30.6	43.9	22.2	30.6	40.6

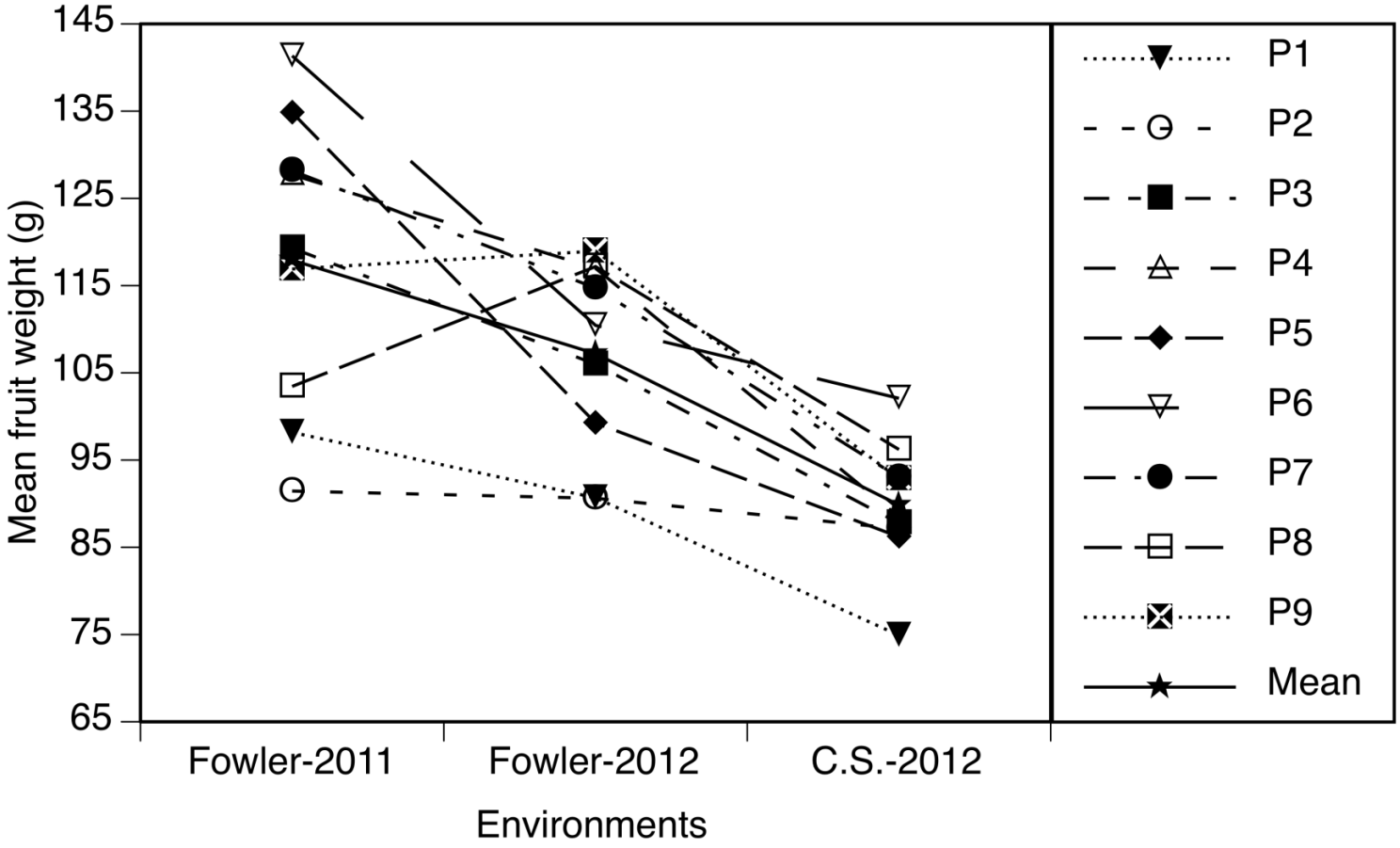
[y]Previous year

APPENDIX B

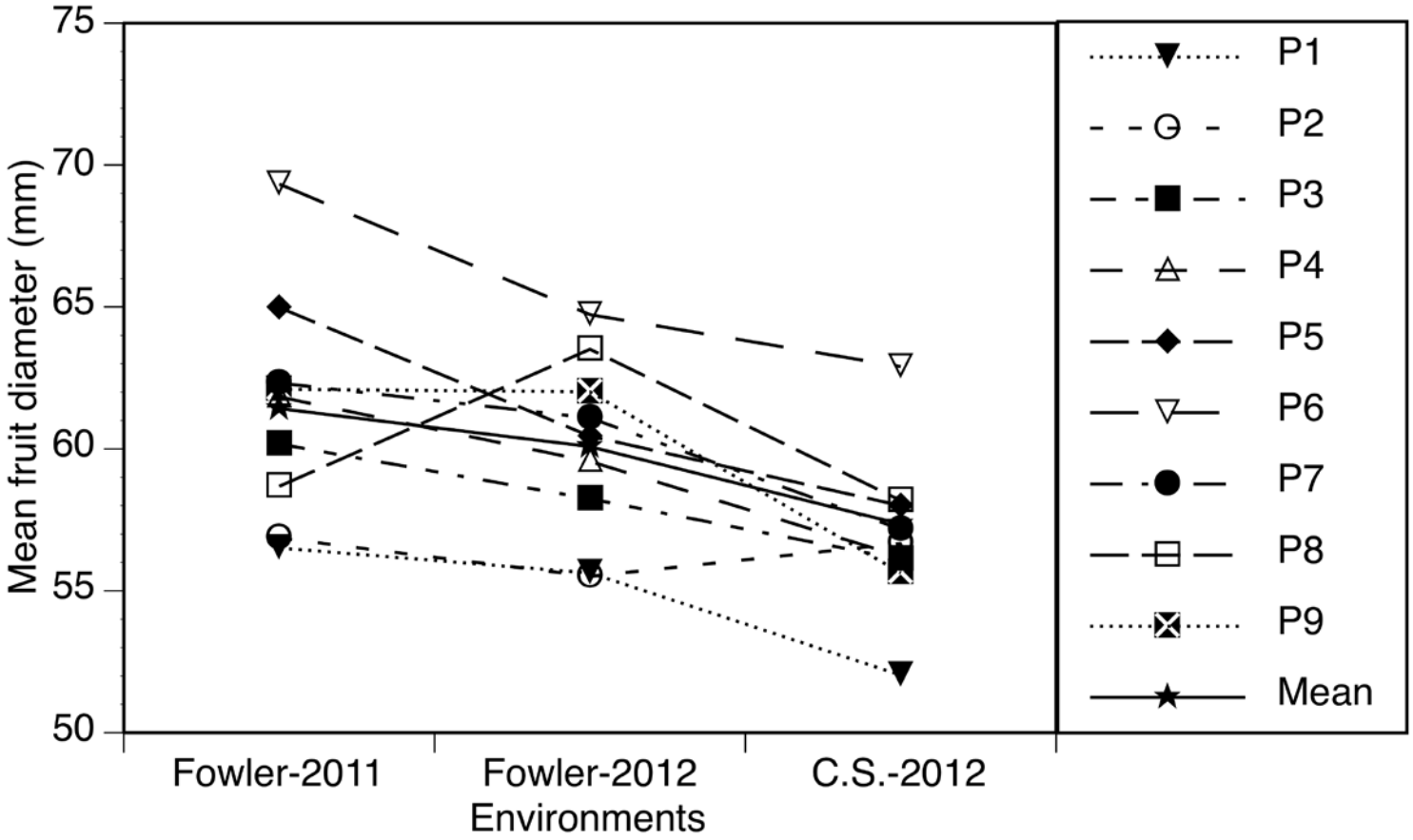


B-1. Response of progenies on a mean basis for fruit red blush across environments: Fowler, 2011; Fowler, 2012; College Station 2012.

Fruit red blush visually based on % coverage of red blush on skin using 0-5 scale (0 = 0% red coverage, 1 = 1%-20%, 2 = 21%-50%, 3 = 51%-80%, 4 = 81%-99%, 5 = 100%).

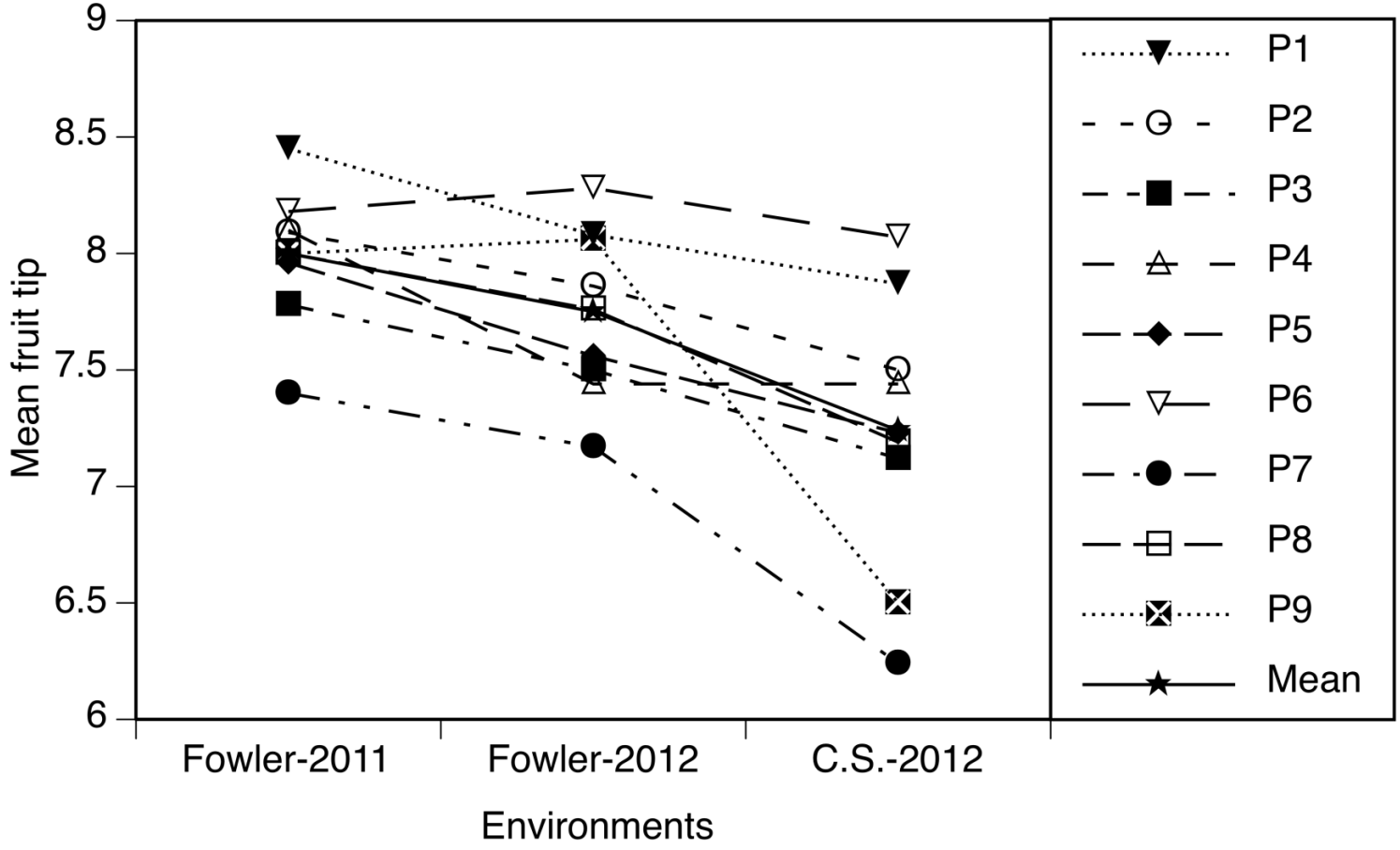


B-2. Response of progenies on a mean basis for fruit weight across environments: Fowler, 2011; Fowler, 2012; College Station 2012. Fruit weight in grams.



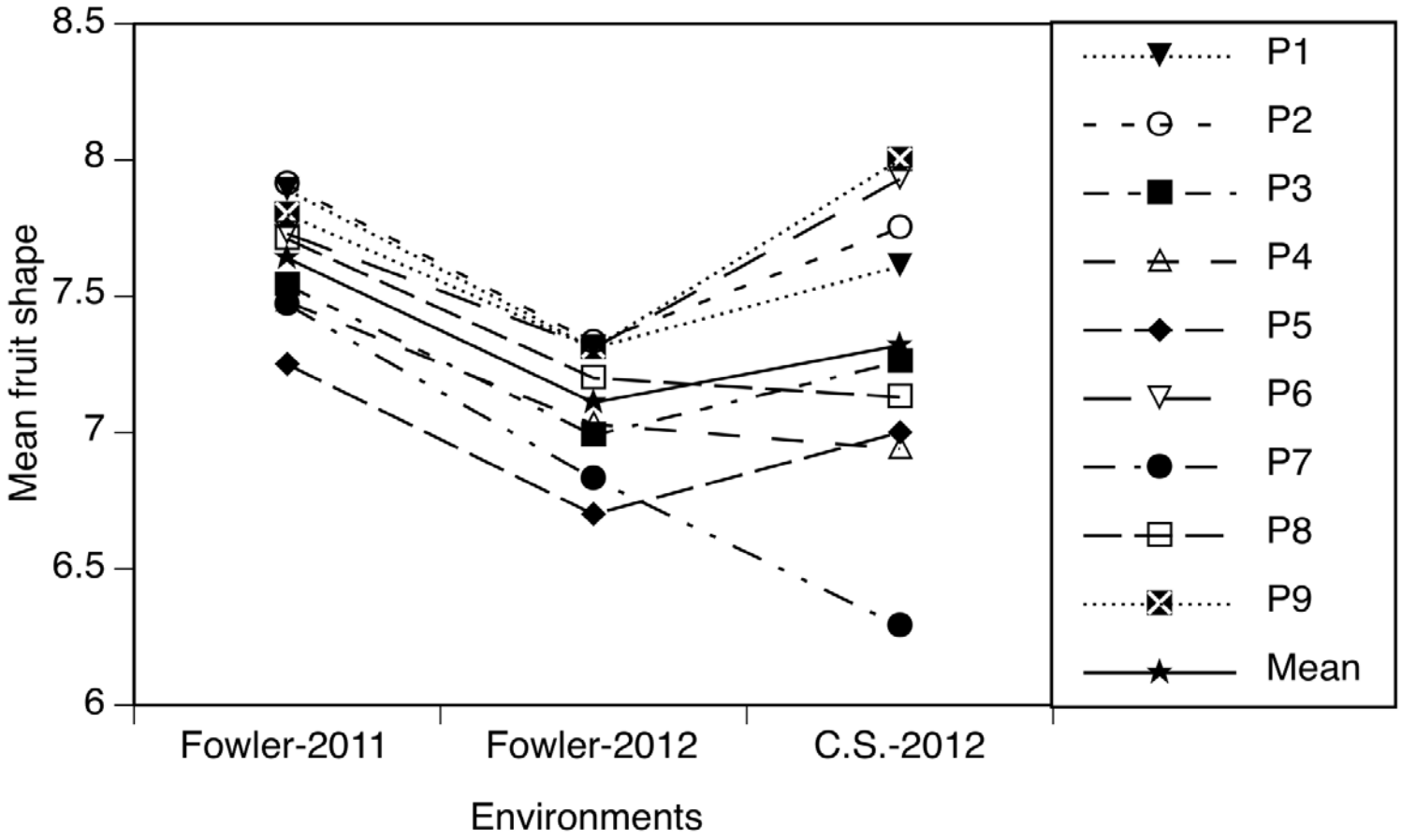
B-3. Response of progenies on a mean basis for fruit diameter across environments: Fowler, 2011; Fowler, 2012; College Station 2012.

Fruit diameter in millimeters.



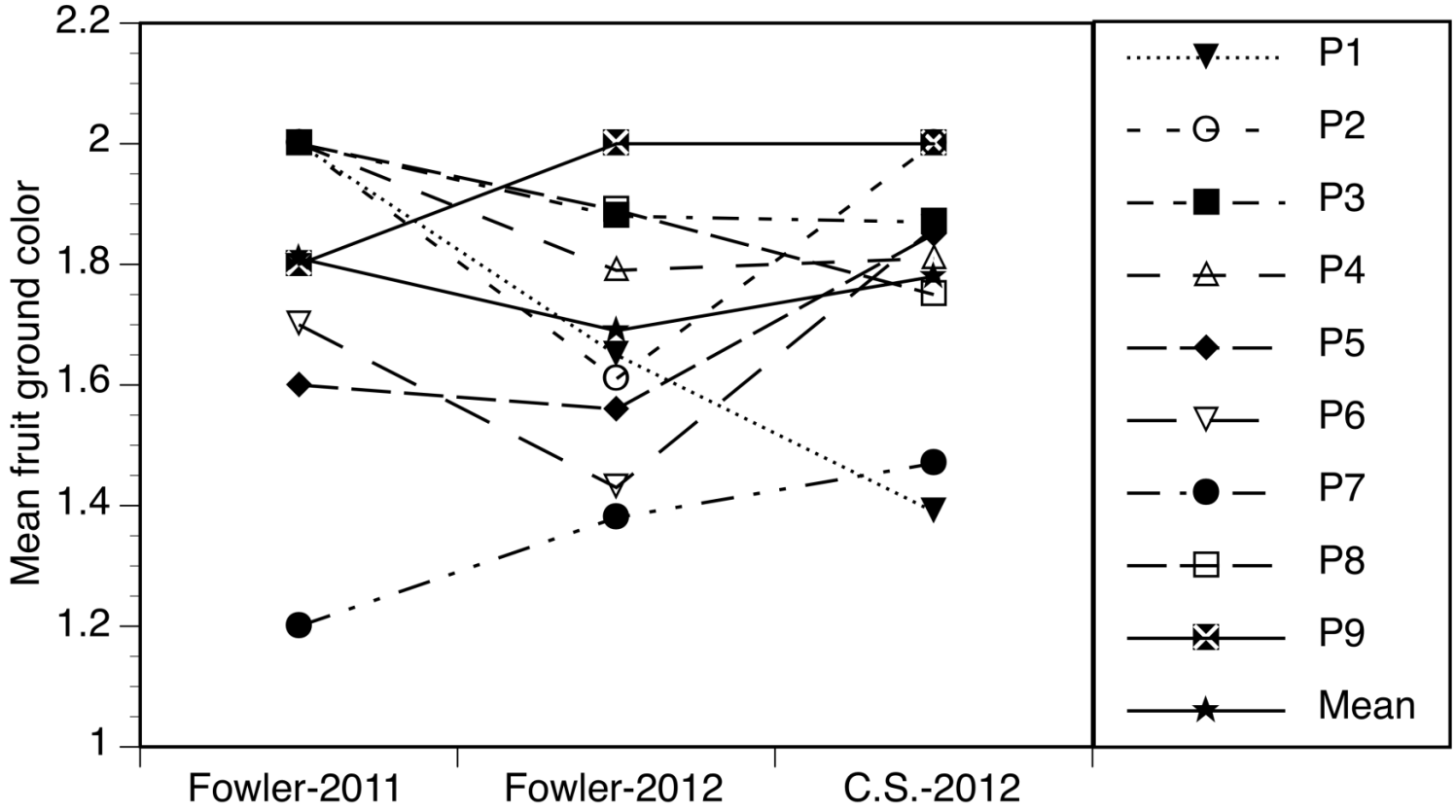
B-3. Response of progenies on a mean basis for fruit tip across environments: Fowler, 2011; Fowler, 2012; College Station 2012.

Fruit tip visually based on 0-9 scale (6 or lower = very prominent fruit tip, 9 = completely oblate fruit tip.



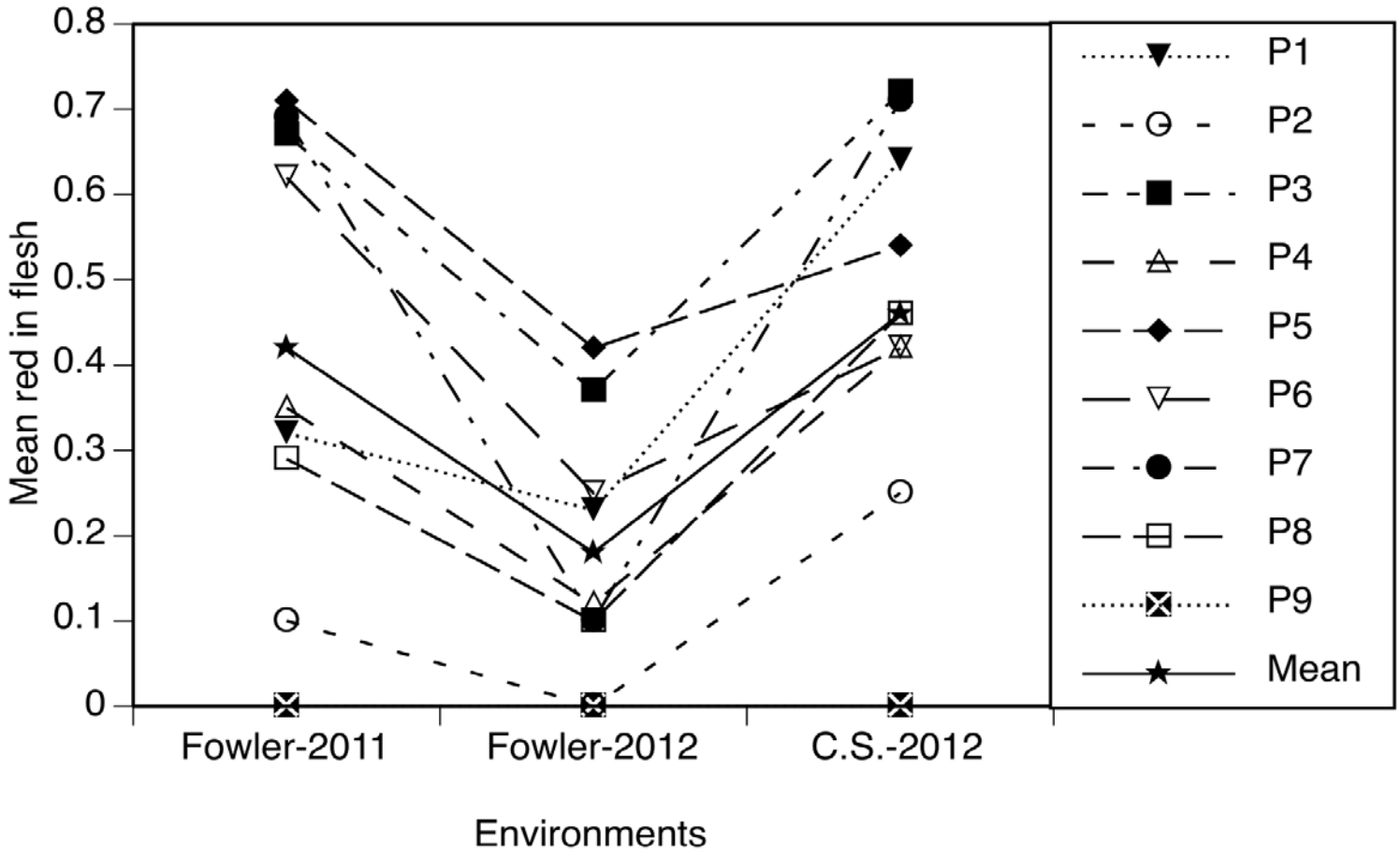
B-4. Response of progenies on a mean basis for fruit shape across environments: Fowler, 2011; Fowler, 2012; College Station 2012.

Fruit shape visually based on 0-9 scale (6 or lower = large suture bulge and prominent tip, 9 = no pronounced suture and oblate tip.



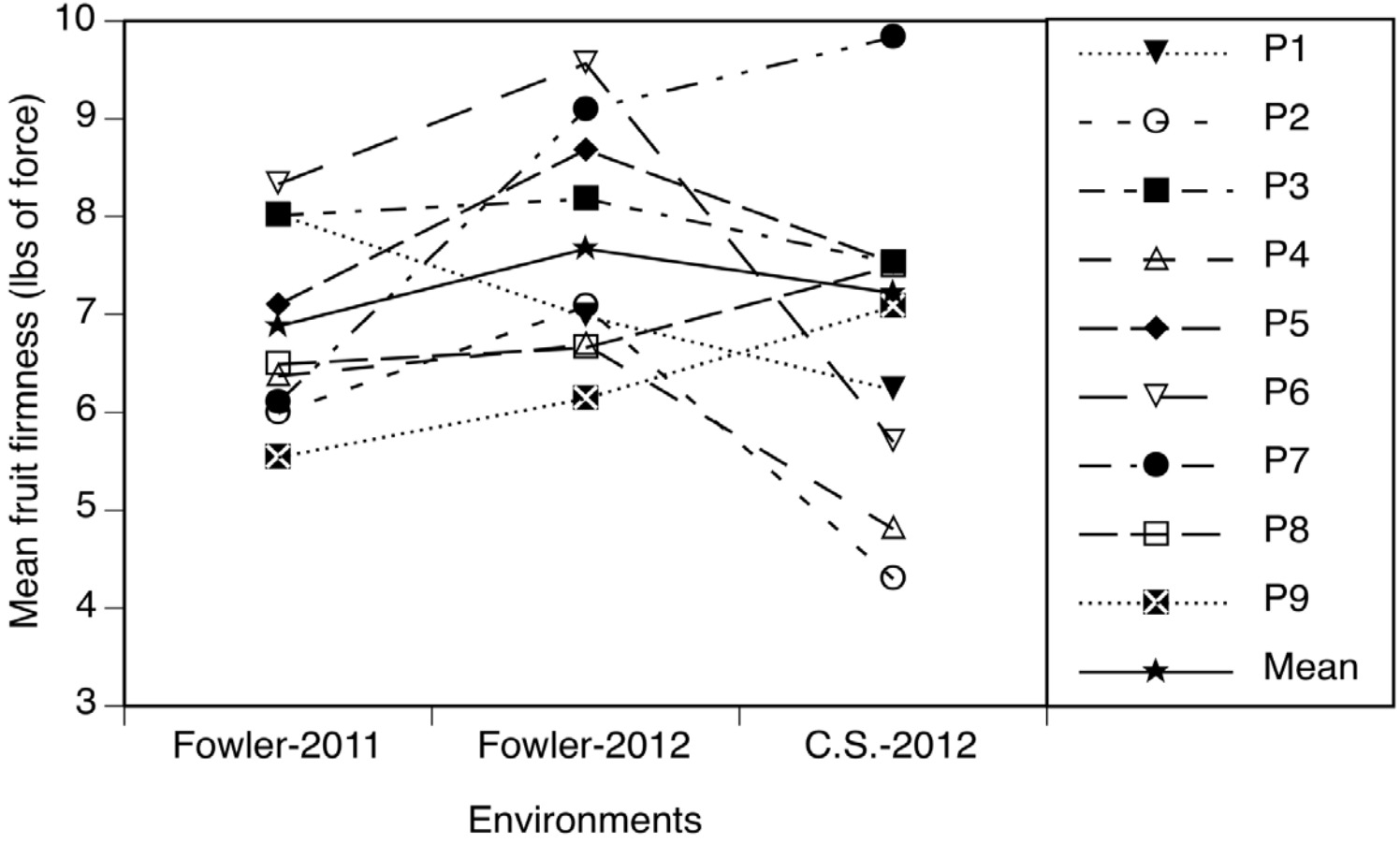
B-5. Response of progenies on a mean basis for fruit ground color across environments: Fowler, 2011; Fowler, 2012; College Station 2012.

Fruit firmness as pounds of force. Fruit ground color expressed as amount of green color based on 0-2 scale (0 = green, 2 no green); fruit flesh color expressed as amount of green color based on 0-2 scale (0 = green, 2 = no green).

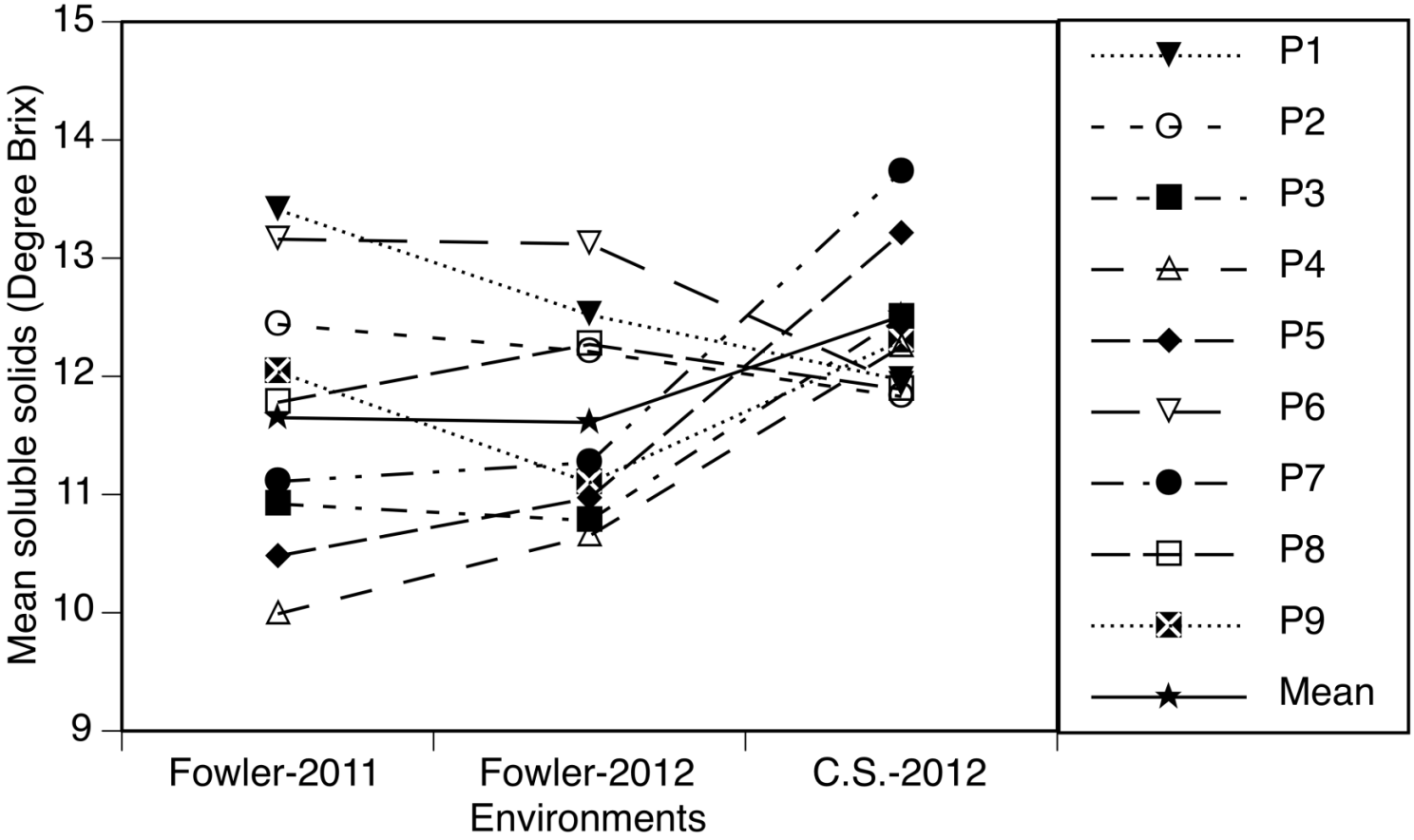


B-6. Response of progenies on a mean basis for red in flesh across environments: Fowler, 2011; Fowler, 2012; College Station 2012.

Red in flesh based on % red overlay of fruit flesh using 0-10 scale (0 = 0% red overlay, 10 = 100% red overlay).

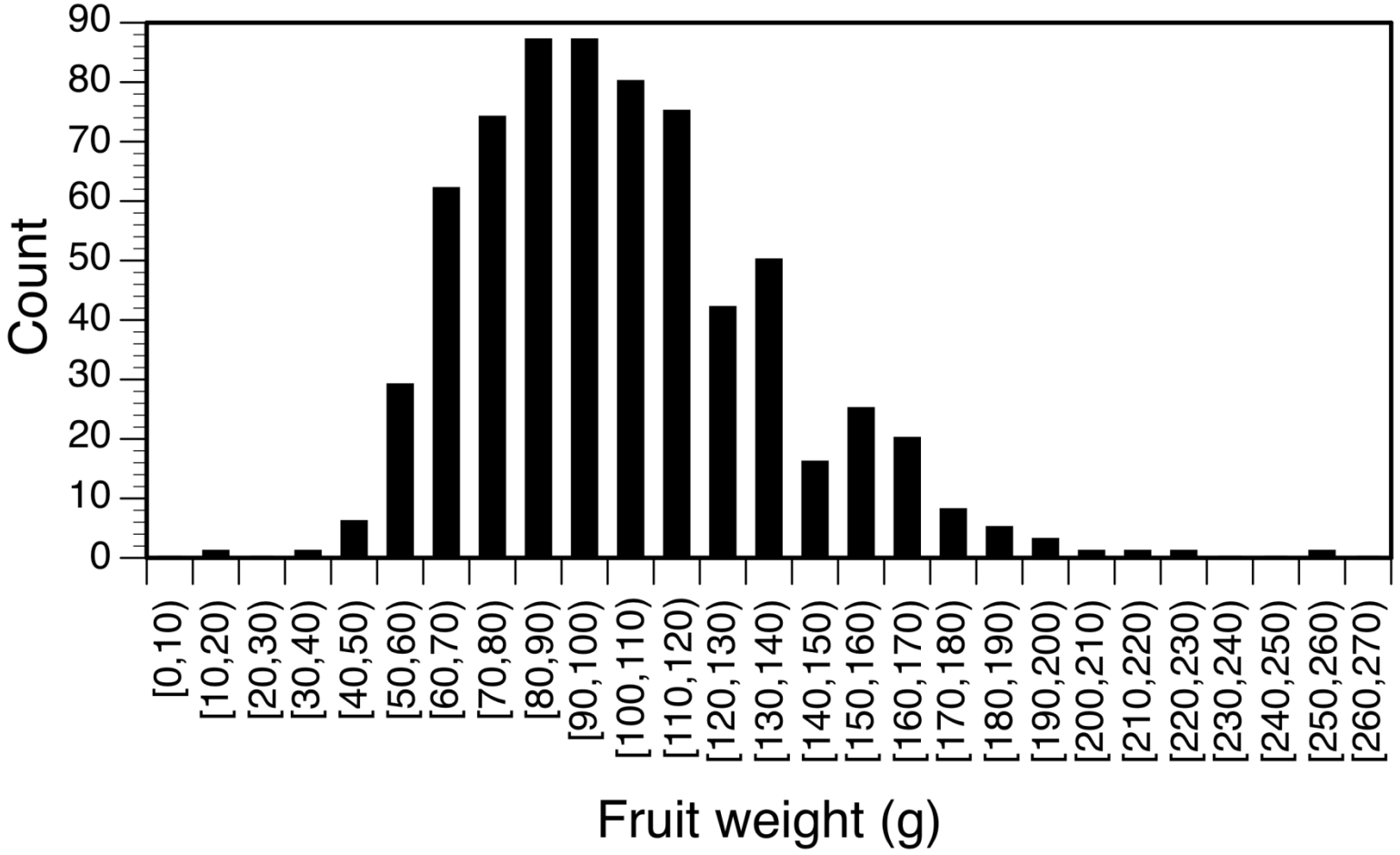


B-7. Response of progenies on a mean basis for fruit firmness across environments: Fowler, 2011; Fowler, 2012; College Station 2012. Fruit firmness as pounds of force.



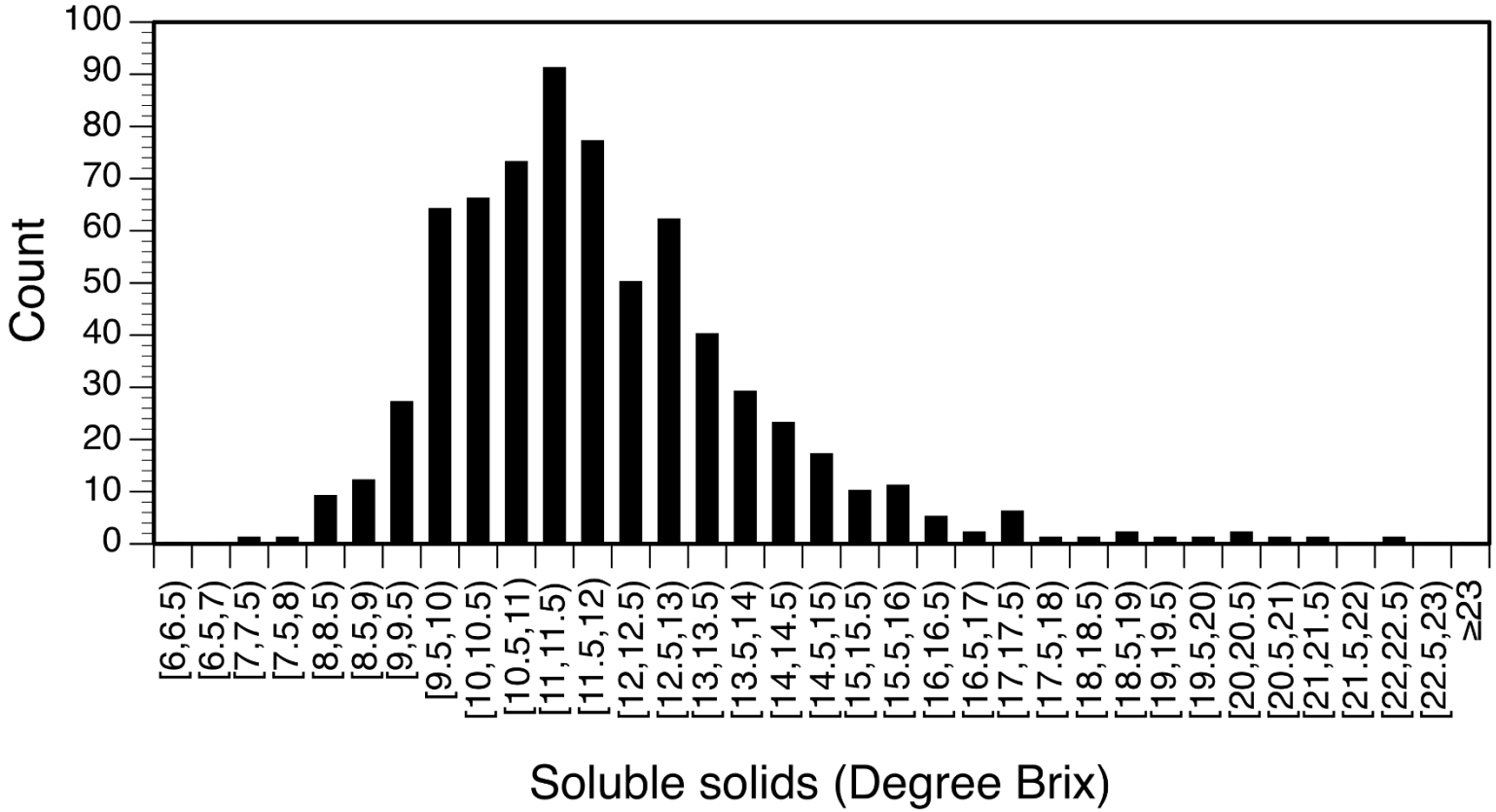
B8. Response of progenies on a mean basis for soluble solids across environments: Fowler, 2011; Fowler, 2012; College Station 2012.

Soluble solids in °Brix



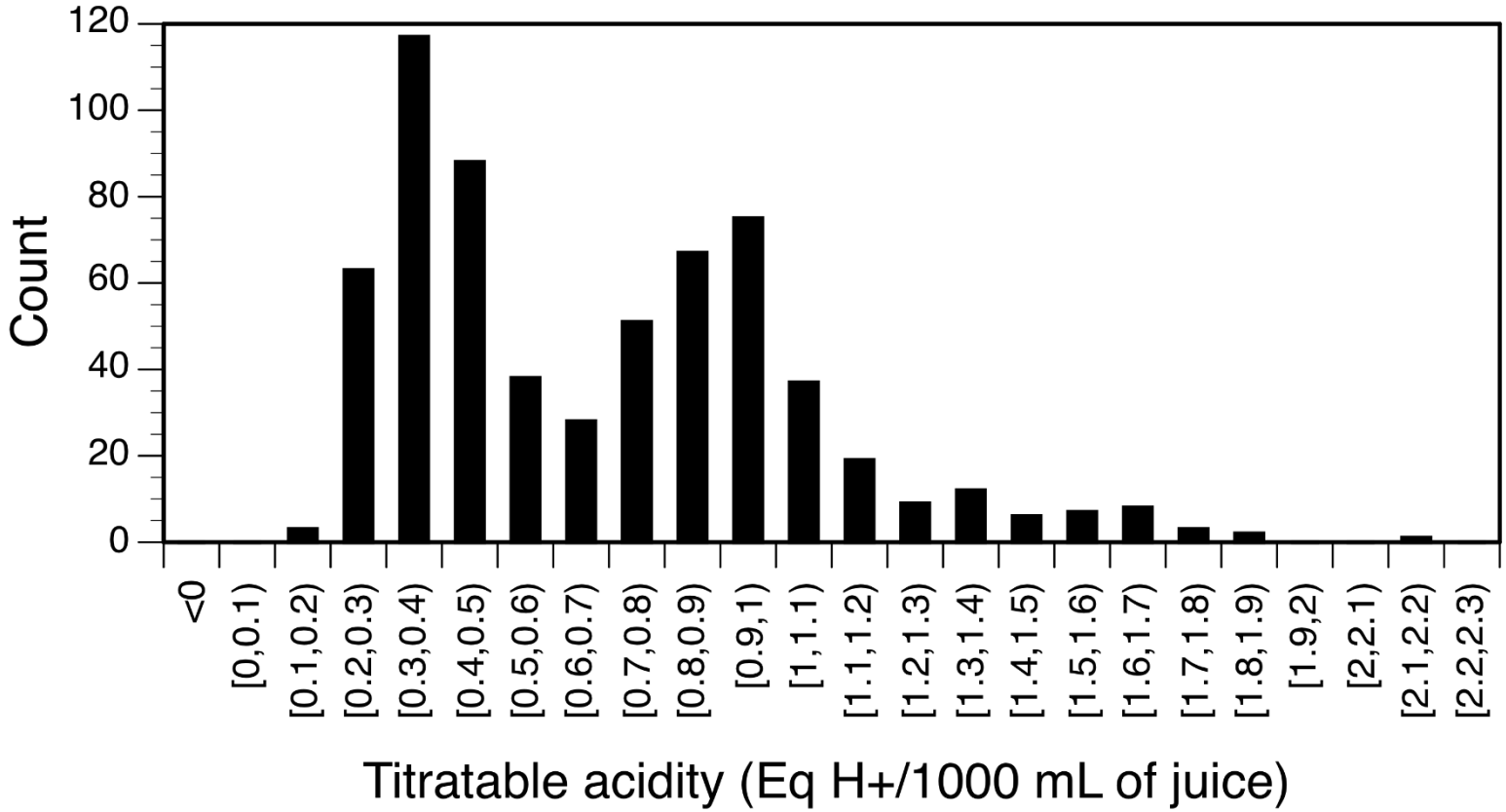
B-9. Distribution of fruit weight for nine progenies for two years at Fowler, CA and one year at College Station, TX.

Fruit weight in grams.



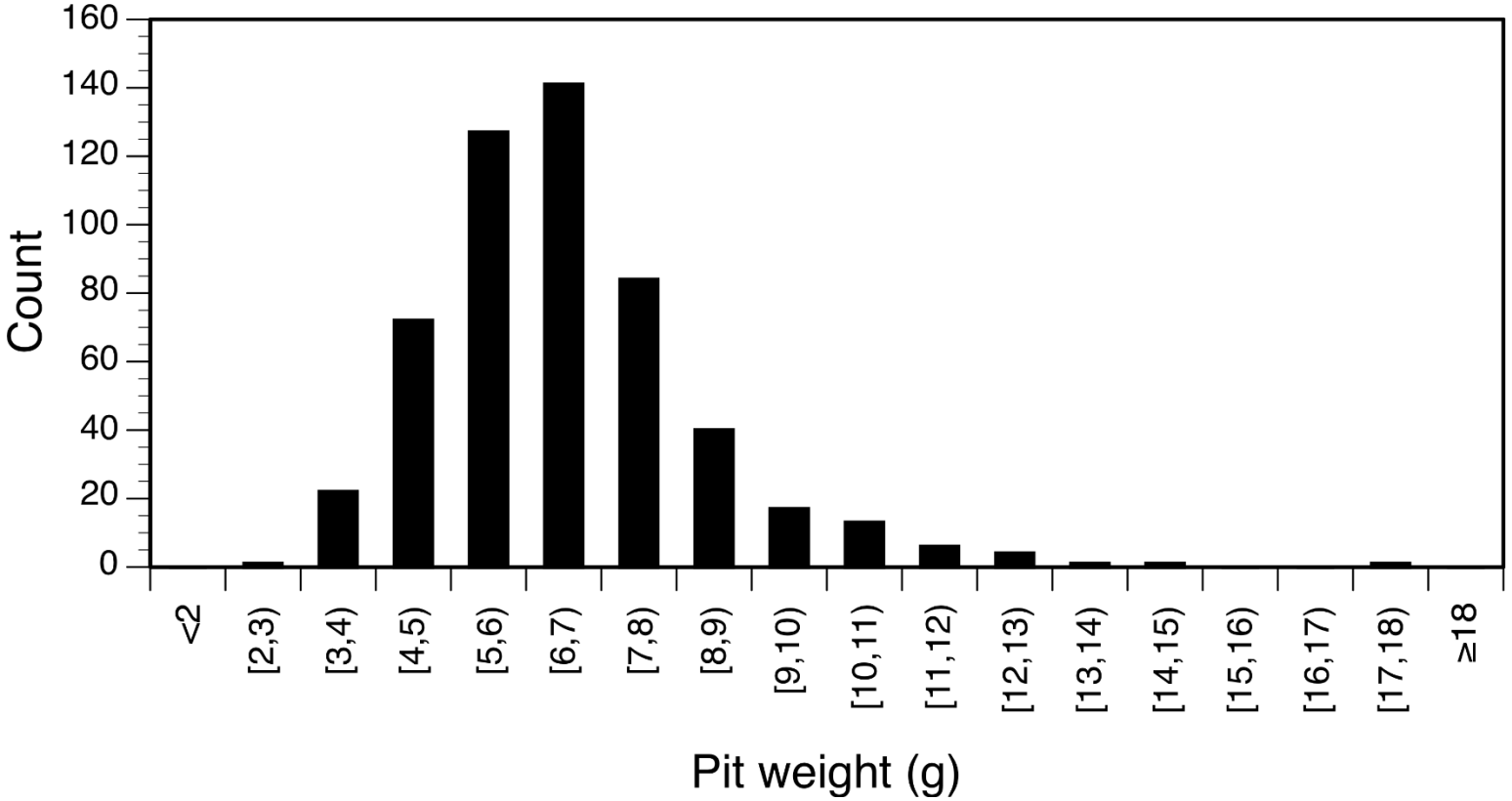
B-10. Distribution of fruit soluble solids for nine progenies for two years at Fowler, CA and one year at College Station, TX.

Soluble solids in °Brix.



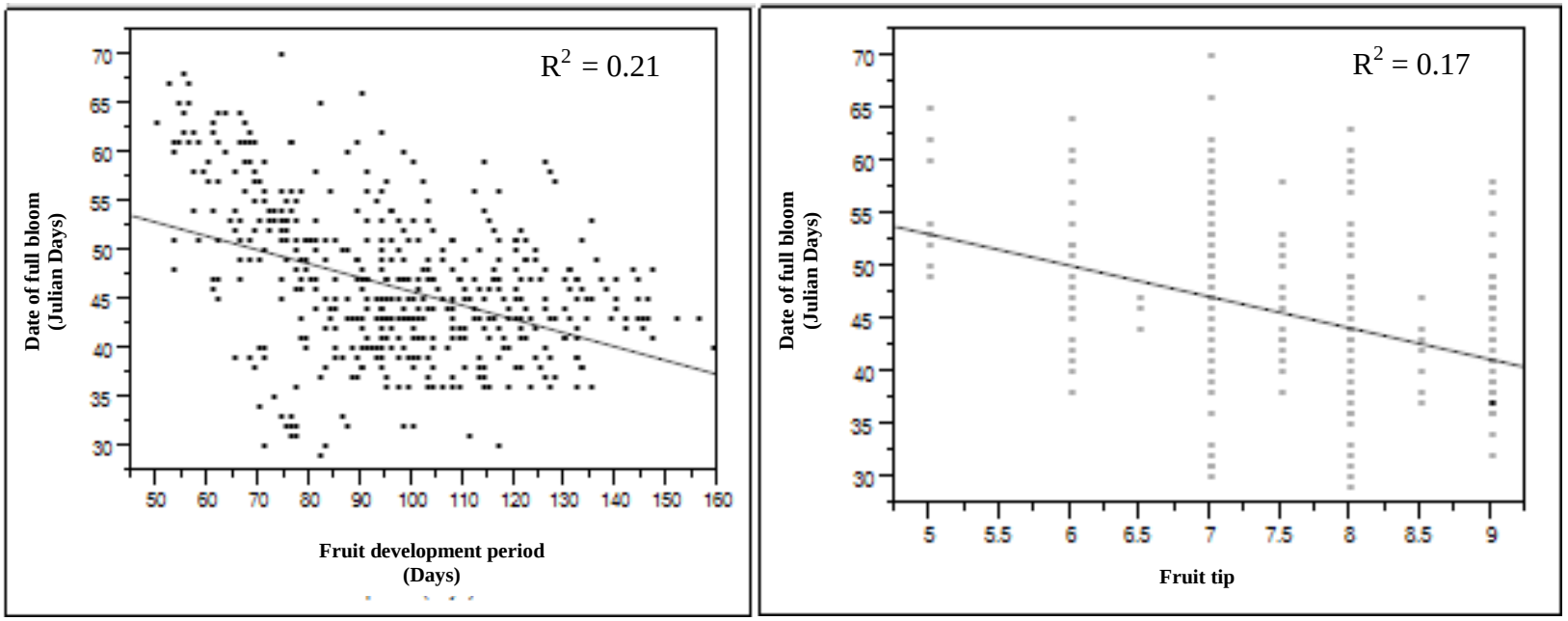
B-11. Distribution of titratable acidity evaluated for nine progenies for two years at Fowler, CA and one year at College Station, TX.

Titratable acidity expressed as Eq H^+/1000 mL of juice.



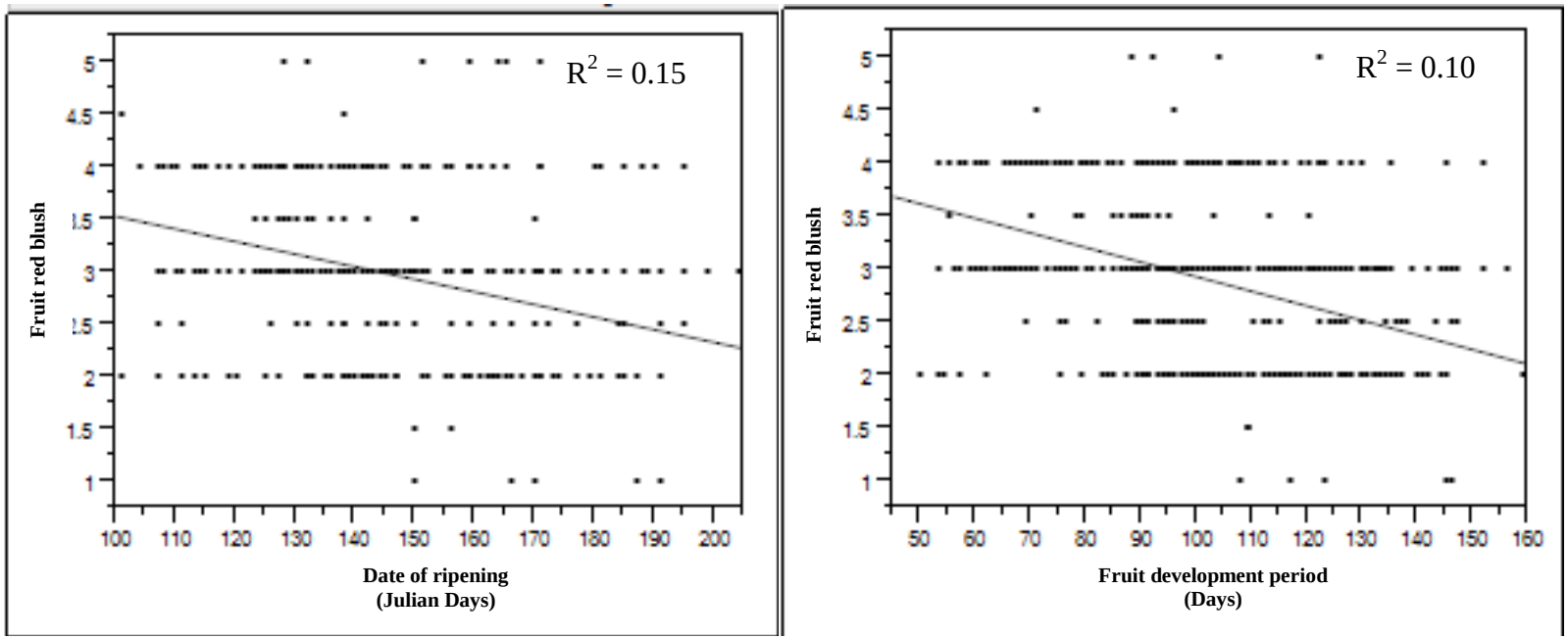
B-12. Distribution of pit weight evaluated for nine progenies for two years at Fowler, CA and one year at College Station, TX.

Pit weight in grams.



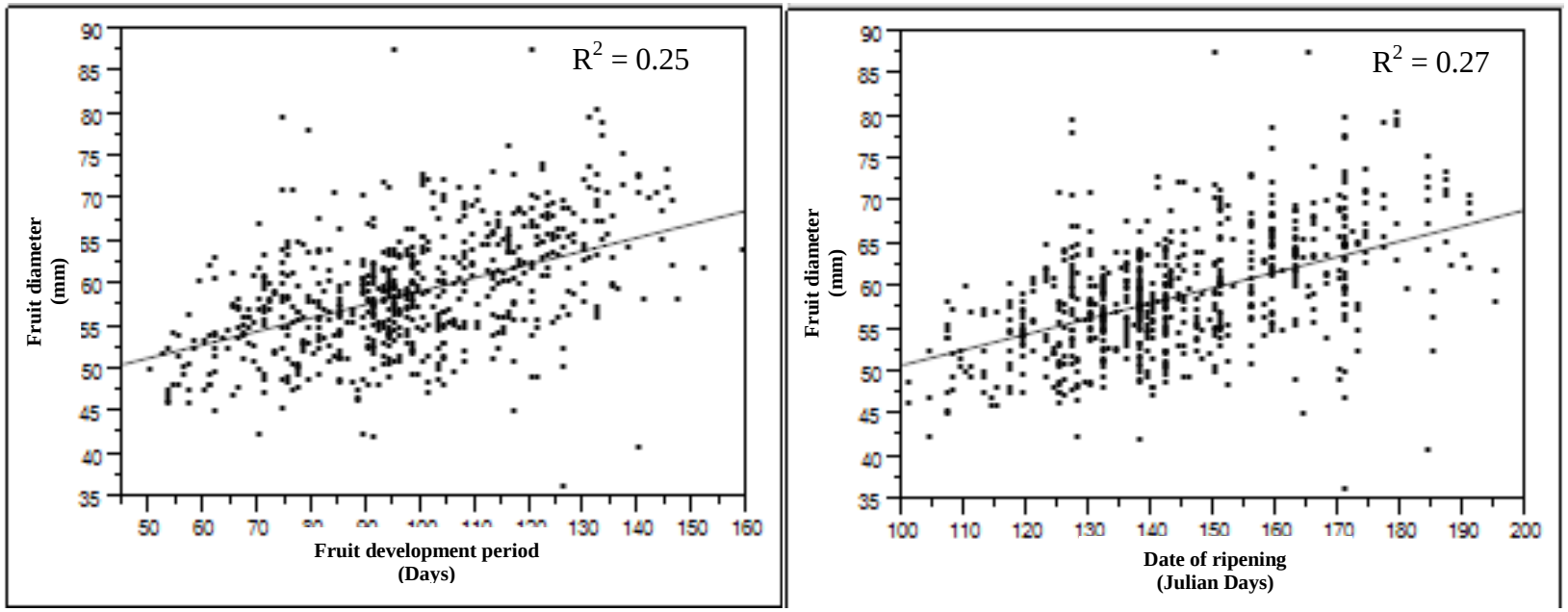
B-13a & B-13b. Left: Scatter plot depicting correlation between date of full bloom and fruit development period. Right: Scatter plot depicting correlation between date of full bloom and fruit tip.

Date of full bloom in Julian Days; fruit development period in days; fruit tip visually based on 0-9 scale (6 or lower = very prominent fruit tip, 9 = completely oblate fruit tip).



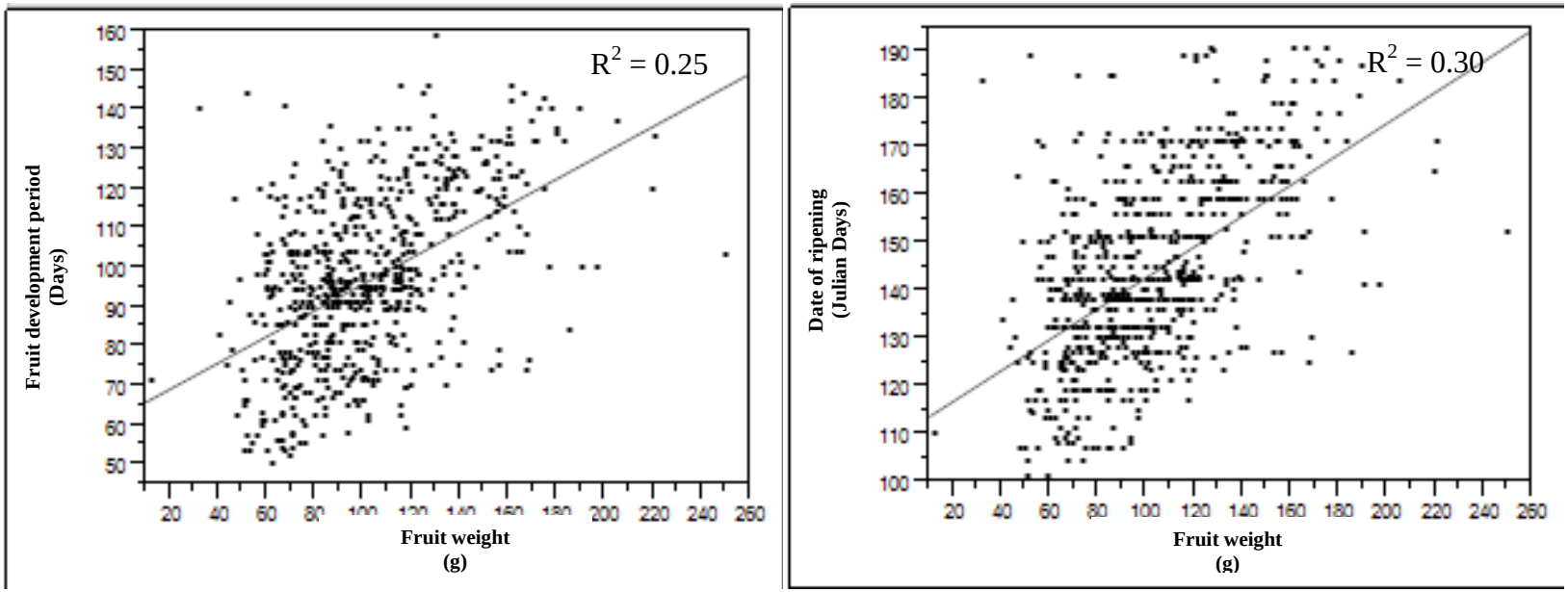
B-14a & B-14b. Left: Scatter plot depicting correlation between fruit red blush and date of ripening. Right: Scatter plot depicting correlation between fruit red blush and fruit development period.

Fruit red blush visually based on % coverage of red blush on skin using 0-5 scale (0 = 0% red coverage, 1 = 1%-20%, 2 = 21%-50%, 3 = 51%-80%, 4 = 81%-99%, 5 = 100%); date of ripening in Julian Days; fruit development period in days.



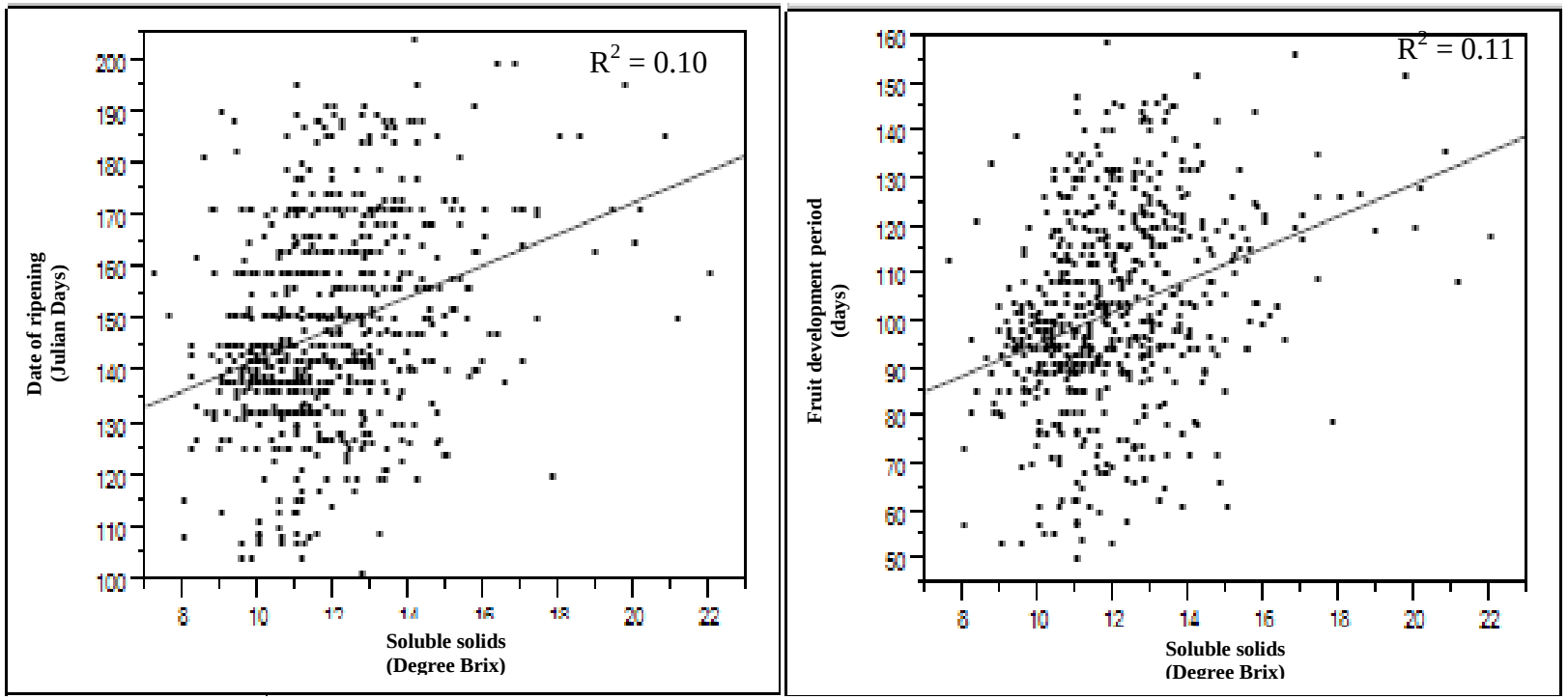
B-15a & B-15b. Left: scatter plot depicting correlation between fruit diameter and fruit development period. Right: scatter plot depicting correlation between fruit diameter and date of ripening.

Fruit diameter in mm; fruit development period in days; date of ripening in Julian Days.



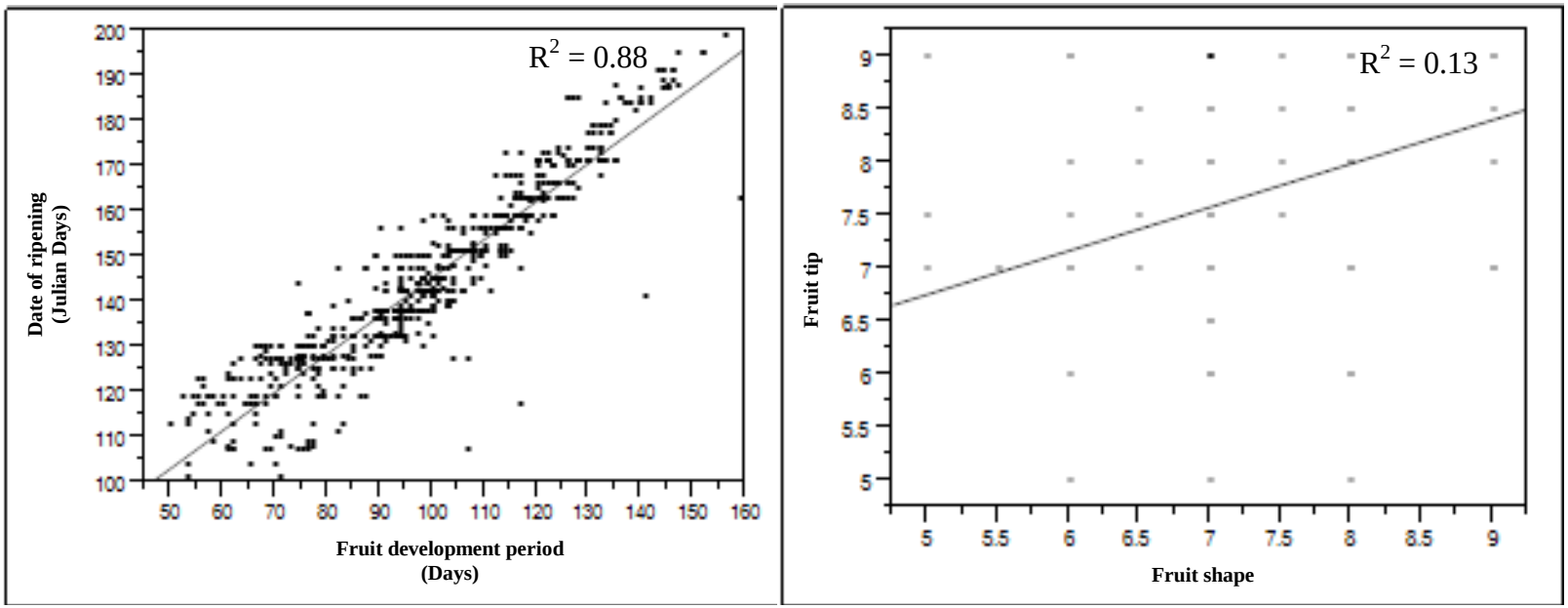
B-16a & B-16b. Left: scatter plot depicting correlation between fruit development period and fruit weight. Right: scatter plot depicting correlation between date of ripening and fruit weight.

Fruit development period in days; fruit weight in grams; date of ripening in Julian Days.



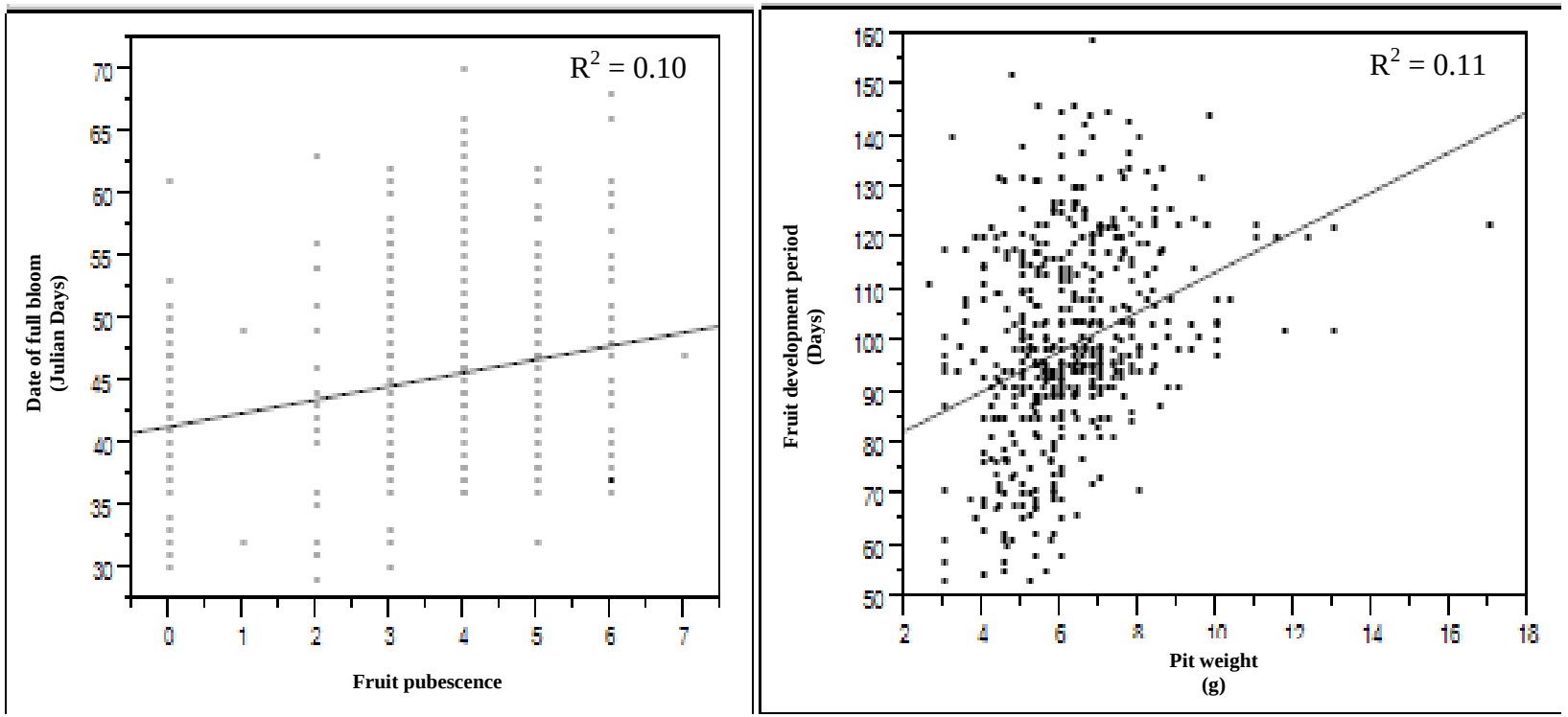
B-17a & B-17b. Left: scatter plot depicting the correlation between date of ripening and soluble solids. Right: scatter plot depicting the correlation between fruit development period and soluble solids.

Date of ripening in Julian Days; soluble solids in °Brix; fruit development period in days.



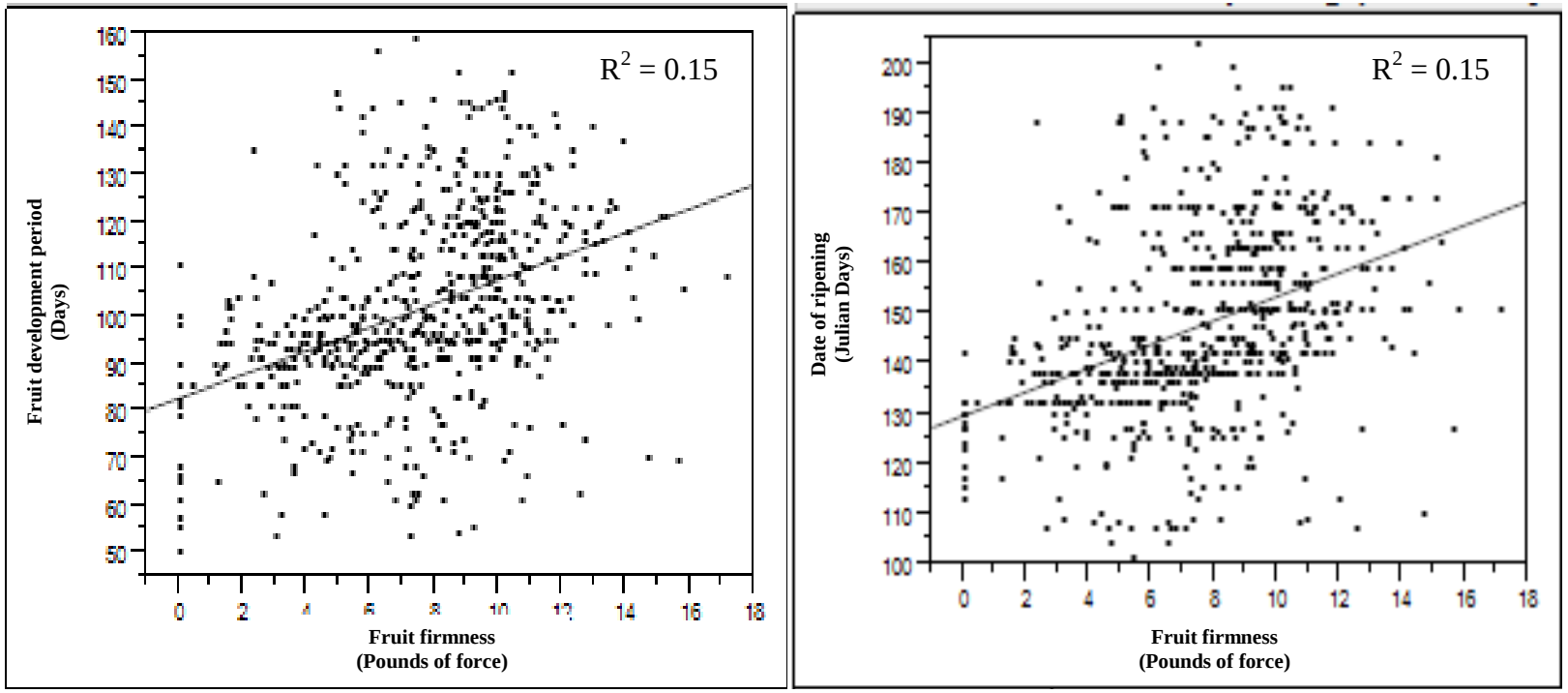
B-18a & B-18b . Left: Scatter plot depicting the correlation between date of ripening and fruit development period. Right: scatter plot depicting the correlation between fruit tip and fruit shape.

Date of ripening in Julian Days; fruit development period in days; fruit tip visually based on 0-9 scale (6 or lower = very prominent fruit tip, 9 = completely oblate fruit tip); fruit shape visually based on 0-9 scale (6 or lower = large suture bulge and prominent tip, 9 = no pronounced suture and oblate tip.



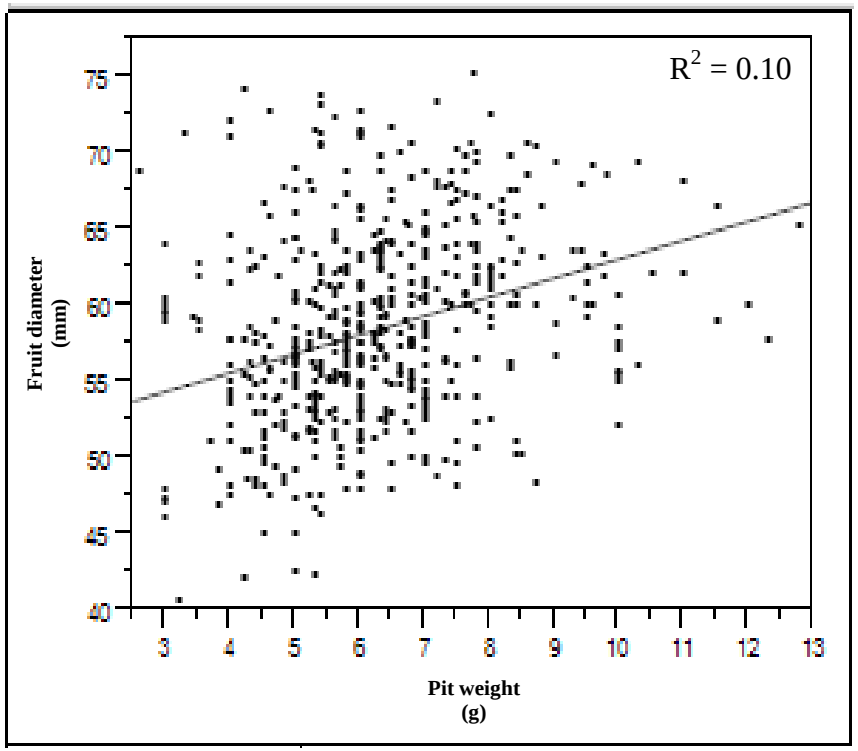
B-19a & B-19b. Left: scatter plot depicting the correlation between date of full bloom and fruit pubescence. Right: scatter plot depicting the correlation between fruit development period and pit weight.

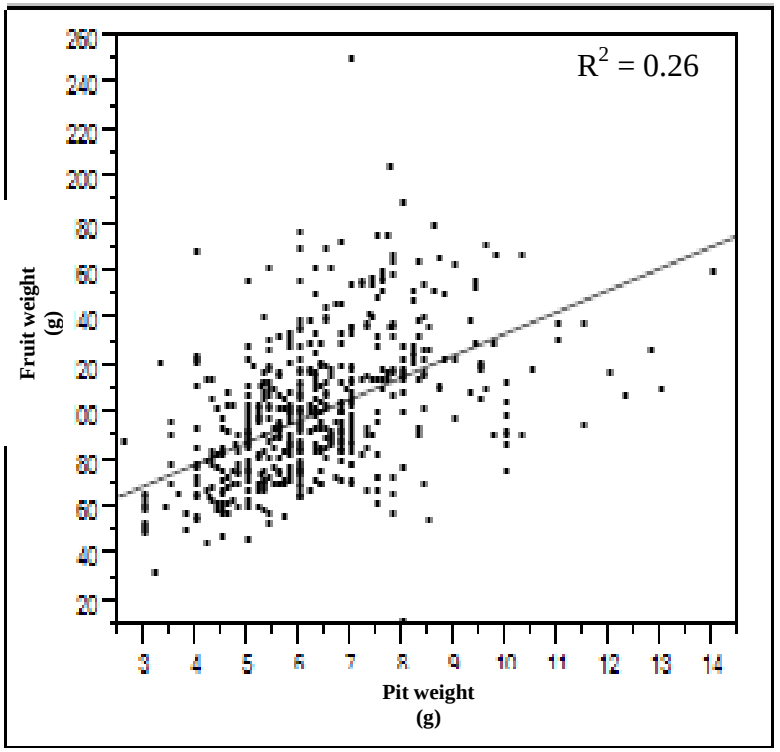
Date of full bloom in Julian Days; fruit pubescence visually based on 0-9 scale (0 = no pubescence, 6 or higher = greater pubescence than modern cultivars; fruit development period in days; pit weight in grams.



B-20a & B-20b. Left: scatter plot depicting the correlation between fruit development period and fruit firmness. Right: scatter plot depicting the correlation between date of ripening and fruit firmness.

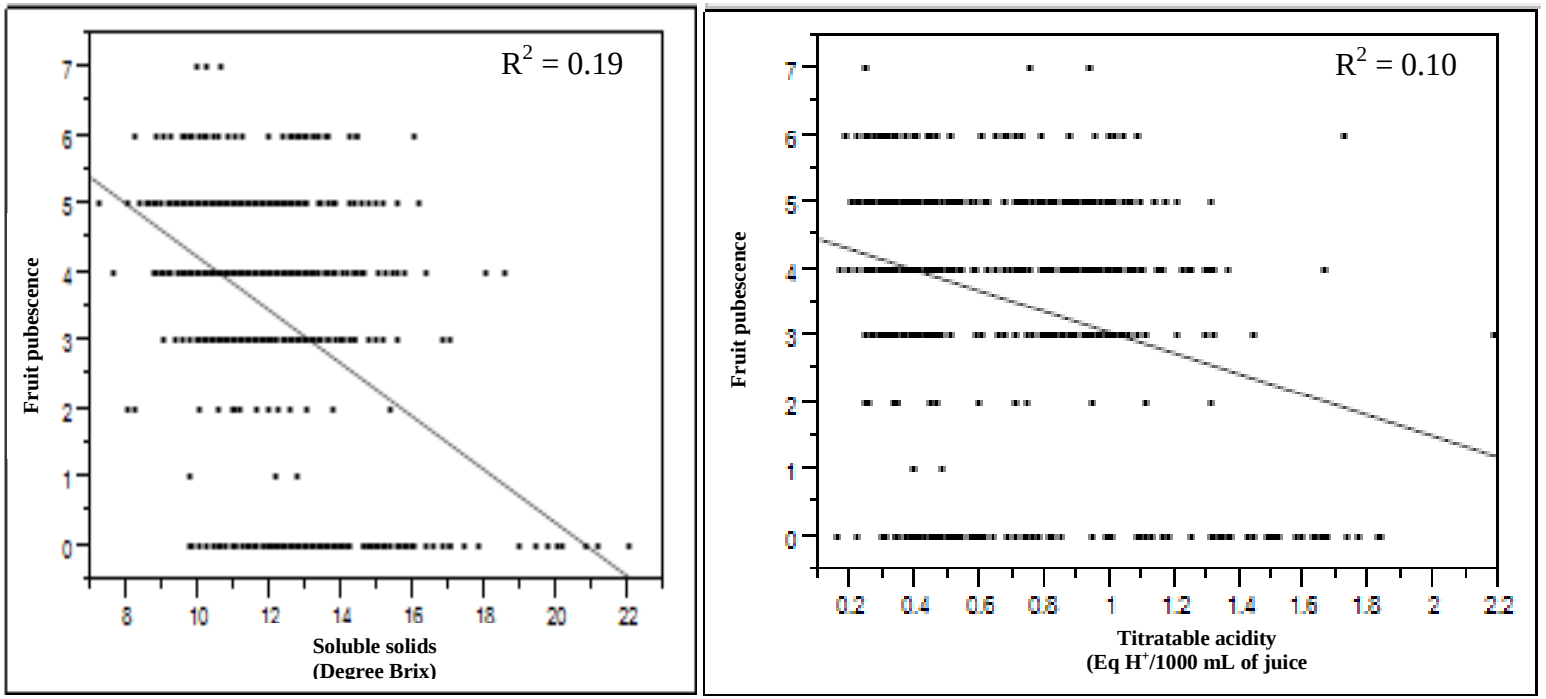
Fruit development period in days; firmness as pounds of force; date of ripening in Julian days.





B-21a & B-21b. Left: scatter plot depicting the correlation between fruit diameter and pit weight. Right: scatter plot depicting the correlation between fruit weight and pit weight.

Fruit diameter in mm; pit weight in grams; fruit weight in grams.



B-22 a & B-22b. Left: scatter plot depicting the correlation between fruit pubescence and soluble solids. Right: scatter plot depicting the correlation between fruit pubescence and titratable acidity.

Fruit pubescence visually based on 0-9 scale (0 = no pubescence, 6 or higher = greater pubescence than modern cultivars); soluble solids in °Brix; titratable acidity as H^+/1000 mL of juice.