

Heritability, Genetic and Phenotypic Correlations, and Predicted Selection Response of Quantitative Traits in Peach: II. An Analysis of Several Fruit Traits

Valdomiro A.B. de Souza¹ and David H. Byrne

Department of Horticultural Sciences, Texas A&M University, College Station, TX 77843-2133

Jeremy F. Taylor

Department of Animal Science, Texas A&M University, College Station, TX 77843-2133

ADDITIONAL INDEX WORDS. *Prunus persica*, quantitative inheritance, multiple trait selection, fruit breeding

ABSTRACT. Thirteen peach [*Prunus persica* (L.) Batsch] fruit characteristics were investigated for 3 years, 1993, 1994, and 1995, in College Station, Texas, to determine heritability, genetic and phenotypic correlations, and predicted response to selection. Seedlings of 108 families resulting from crosses among 42 peach cultivars and selections were used in the evaluations. A mixed linear model, with years treated as fixed and additive genotypes as random factors, was employed to analyze the data. Best linear unbiased prediction (BLUP) was used to estimate fixed effects. Restricted maximum likelihood (REML) was used to estimate variance components, and a multiple trait model was used to estimate genetic and phenotypic covariances between traits. Genetic and phenotypic correlations ≥ 0.65 and < 0.30 were considered strong or very strong and weak, respectively. Date of ripening, fruit development period (FDP) and date of full bloom had the highest heritability (h^2) estimates, 0.94, 0.91, and 0.78, respectively. Fruit cheek diameter and titratable acidity ($h^2 = 0.31$) were the traits with the lowest estimates. Fruit development period, fruit blush, and date of ripening had the highest predicted selection responses, whereas fruit suture, fruit cheek, L/W12 (ratio fruit length to average fruit diameters), and fruit tip had the lowest values. Most genetic correlations were ≥ 0.30 and were, in general, much higher than the corresponding phenotypic correlations. All four measures of fruit size were genetically and phenotypically very strongly correlated. Important genetic correlation estimates were also observed for date of ripening with FDP ($r_a = 0.93$), date of ripening and FDP with fruit blush ($r_a = -0.77$, $r_a = -0.72$), SS (percent soluble solids) ($r_a = 0.63$, $r_a = 0.62$) and TA ($r_a = 0.55$, $r_a = 0.64$), and SS with TA ($r_a = -0.56$). Direct selection practiced solely for early ripening and short FDP is expected to have a greater effect on correlated traits than direct selection for early bloom and large fruit mass.

The success in any crop improvement program depends, among other factors, on the amount of genetic variability available and the methods used for its use. Usually, this is accomplished by selecting and intermating, each generation, only those individuals that show ability to produce superior progeny (Hansche, 1983). Knowledge of genetic parameters such as variances, heritabilities, and correlations among characters under selection are very useful to make predictions of genetic progress among offspring especially when parental genotypes are selected on the basis of their own performance (Falconer, 1989). Heritability also may provide information for examining major changes in amount and nature of genetic variability through generations (Hansche et al., 1966). Heritability, like genetic variances, is a property not only of a character, but also of the population, of the environmental conditions to which the individuals are submitted, and of the way in which the phenotype is measured (Falconer, 1989; Nyquist, 1991). Narrow sense heritability can be defined as the regression of breeding values on phenotype (Falconer, 1989), or as that fraction of the selection differential expected to be gained when selection is practiced on a defined selection unit (Hanson, 1963).

The estimation of heritability for any character requires the partitioning of the observed variation between genetic effects and environmental effects (Cockerham, 1963). When the phenotypic

variability is large, traits with high heritability values are subject to large genetic gains per generation when selection is applied (Dudley and Moll, 1969; Falconer, 1989; Hansche, 1983; Hesse, 1975; Nyquist, 1991). However, a high heritability value is not a synonym of large selection response, because selection response is the product of heritability and the selection differential (i_s). Thus, even though heritability is high, the response may be small if the selection differential is small (Nyquist, 1991).

In peach and in other fruit crops in general, correlation studies have been few, and most refer to phenotypic or linear correlations rather than genetic correlations (Firoozabady and Olmo, 1987; Hansche et al., 1972; Kester et al., 1977; Luby and Finn, 1986; Mowrey and Sherman, 1986; Rodriguez and Sherman, 1985; 1986; Thompson and Baker, 1993). Only a few investigations reporting on genetic correlations in fruit crop species have been found in the literature (Hansche et al., 1966, 1968; Nassar, 1963; Shaw, 1988; Vileila-Morales et al., 1981) and from those, only one was with peach (Vileila-Morales et al., 1981). Genetic correlation or the correlation between breeding values can result from both pleiotropy or linkage (Falconer, 1989; Mode and Robinson, 1959), while phenotypic correlation which is the correlation between phenotypic values is a nonadditive combination of both genetic and environmental correlations.

Peaches, like most fruit and nut crops, present several experimental difficulties for the breeder who is interested in estimating variance components or functions of them, such as heritability. Not only do experiments consume large amount of space, but also the long juvenility period often makes these investigations expensive and unattractive for the breeder (Hansche, 1983; Hansche and Beres, 1980). Thus, methods of estimating genetic parameters that efficiently make use of the information available from breeding

Received for publication 24 Mar. 1997. Accepted for publication 29 Jan. 1998. Research conducted at Texas A&M University, College Station, TX. A portion of the dissertation submitted by V.A.B. de Souza for the PhD in plant breeding. The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulations, this paper therefore must be hereby marked *advertisement* solely to indicate this fact.

¹Current address: EMBRAPA/CPAMN, Cx. Postal 01, Teresina, PI, Brazil.

programs are extremely useful. In this regard, regression of offspring performance on mid-parent performance has been one of the most useful methods for calculating narrow sense heritability in fruit crops (Falconer, 1989). However, the regression coefficient is an unbiased estimate of the narrow sense heritability only if the inbreeding coefficient of the parents is zero (Fernandez and Miller, 1985). In addition, the regression coefficient inflates heritability estimates when environmental correlation between parent and offspring exists (Cockerham, 1963; Dudley and Moll, 1969; Falconer, 1989). Many other methods based on variance components have also been used for calculating both broad and narrow sense heritabilities in plants (Comstock and Robinson, 1948; Cockerham, 1963; Gordon, 1980; Nyquist, 1991; Robinson et al., 1949). However, for reliable estimates of variance components most of them require well planned experimental designs, which often are expensive and, for fruit tree crops, difficult to apply (Namkoong and Roberds, 1974; Simmonds, 1979).

In the present paper we applied restricted maximum likelihood (REML) to estimate variance components, narrow sense heritability and genetic and phenotypic correlations of 13 peach fruit characteristics. REML is a statistical procedure widely used in animal breeding (Henderson, 1983; Searle, 1971), but its application in plant breeding has been restricted. Most investigations involving REML or other maximum likelihood based procedures in plants have been done by using simulated data (Caro et al., 1985; Huber, 1994; McCutchan et al., 1985; Muse and Anderson, 1978). Only two examples of the use of maximum likelihood-based procedures in fruit crops have been found in the literature (Tancred et al., 1995; Vileila-Morales et al., 1981).

Materials and Methods

EXPERIMENTAL MATERIALS. The breeding material used was fresh market, melting flesh peach germplasm from the Texas A&M Univ., College Station, peach breeding program. It originated from two different sets of crosses: one made in 1990 (C-90) and established in the field in Spring 1991 and another made in 1991 (C-91) and established in the field in Spring 1992 (Table 1). Seedlings in both blocks were planted 1.5 m between rows and 0.2 m within rows. Most parents used were related to each other to some degree, resulting in an overall inbreeding coefficient of the progeny of 0.23.

EVALUATIONS. The seedlings were evaluated once a year in 1993 and 1994 for C-90 block, and in 1994 and 1995 for C-91 block, when they were 3 and 4 years old. The fruit characteristics evaluated were date of full bloom, date of ripening, fruit development period (FDP), fruit mass, percent soluble solids, fruit acidity, fruit length, suture and cheek diameters, fruit red skin color (blush), tip, and shape. For full bloom and ripe dates, evaluations were done three times a week when most seedlings were blooming or ripening, and twice a week early and late in the blooming or ripening seasons. A seedling was considered at full bloom when $\approx 60\%$ of the flower buds were opened and ripe when 15% to 20% of fruit were in the soft stage. The number of days for both characters were given as days from 1 Jan. Fruit development period was measured in days as the interval between date of full bloom and date of ripening. Fruit length, cheek and suture diameters were measured in centimeters with a standard caliper. Fruit blush, tip and shape were subjectively evaluated by using a score scale ranging from 0 to 9. For fruit blush, a score of 0 = 0% to 9% red color, and a score of 9 = 90% to 100% red color. Fruit with large and pronounced tips received a score of 4 and lower and fruit with no tips a score of 9 for fruit tip. For fruit shape, fruit with large suture bulges and large and pronounced tips received a score of 4 or lower, and round or slightly oblong fruit with no suture or tip a score of 9. Fruit

shape was also measured as the ratio of fruit length to the average fruit diameter. The higher the ratio indicates a less desirable fruit shape. Average fruit mass was measured in grams. All these fruit measurements were based on a five-fruit sample per seedling. Some seedlings which set poorly, were represented by as few as one fruit. Fruit samples were held in the freezer (-2°C) until analyzed.

CHEMICAL ANALYSIS. Before analysis, fruit samples were thawed (4 h at room temperature). Then they were peeled and the juice extracted by manually squeezing the fruit into a 400 mL plastic beaker. This was filtered with a plastic filter (one millimeter screen). The percent soluble solids (degrees Brix) was determined with a Bausch & Lomb AbbE refractometer with automatic temperature compensation. Titratable acidity was determined by pipetting 10 mL of filtered juice into a 250-mL beaker, diluting it to 125 mL with distilled water, and titrating with 0.1 N NaOH to pH 8.2. The results were expressed as equivalents of anhydrous malic acid per liter of juice ($\text{eq H}^+/\text{L}$). (Byrne et al., 1991). The conversion to titratable acidity (TA) was given by the formula $\text{TA} = [(\text{mL NaOH} \times \text{N} \times 0.067045) \div \text{mL juice}] \times 1000$, where mL NaOH = mL NaOH used in titration, N = normality of NaOH, and 0.067045 = meq weight of malic acid.

STATISTICAL ANALYSIS. The data for bloom date, ripe date, FDP, fruit mass, percent soluble solids, TA, fruit tip, and shape were transformed according to procedures described by Box and Cox (1964) to improve normality. The results for year effects and predicted selection response were transformed back to the original scale. The procedures are presented in Souza et al. (1997).

The analyses were performed using the mixed linear model $y = X\beta + Zu + Zpe^* + e$, where y is the vector of observations of length N , β is an unknown vector of length p containing fixed effects, u is a nonobservable vector of length g containing random effects (breeding values), pe^* is the vector of length g containing uncorrelated random effects (permanent environment and nonadditive genetic effects), X is the known $N \times p$ matrix relating observations in Y to elements in b , Z is the known $N \times g$ matrix relating observations in Y to elements in u , and e is the random vector of length N of residuals.

The year effects were estimated by using best linear unbiased prediction (BLUP) (Henderson, 1974, 1975, 1977, 1983). Restricted maximum likelihood (REML) was used to estimate variance components, heritabilities, repeatabilities and genetic and phenotypic covariances (Patterson and Thompson, 1971; Souza et al., 1997).

Table 1. Number genotypes and observations used in variance component and heritability estimates of 13 peach fruit characteristics studied in 108 crosses.

Characters	Genotypes (no.)	Observations (no.)
Date of full bloom	1178	2281
Date of ripening	1125	1988
Fruit development period	1125	1988
Fruit mass	1113	1944
Percent soluble solids	1107	1938
Titratable acidity	1109	1936
Fruit length	1113	1946
Fruit suture	1113	1946
Fruit cheek	1113	1946
L/W ¹²	1113	1946
Fruit blush	1113	1946
Fruit tip	1113	1946
Fruit shape	1113	1946

¹²Ratio of fruit length to average fruit diameter.

Because the sampling variances of the estimated correlations were not available, the discussion of the genetic and phenotypic correlations are based on the magnitude of the estimates as follows: 1) a correlation estimate ≥ 0.65 was considered strong or very strong, 2) a correlation estimate between 0.64 and 0.50 was considered moderately strong, 3) a correlation estimate between 0.49 and 0.30 was considered moderately weak, and 4) a correlation estimate lower than 0.30 was considered weak or very weak.

The predicted response to selection were made with the formula: $R = ih^2s_p$, where R, the expected response per generation, is the difference in mean phenotypic value of the progeny of randomly mated selected parents and the population mean (parental generation) before selection; i, the selection intensity, is the average superiority in phenotypic value of the individuals selected as parents expressed in standard deviations from the population mean (Falconer, 1989; Hansche, 1983); and s_p is the phenotypic standard deviation of the parental generation before selection. The predictions were based on the transformed phenotypic standard deviations and were estimated considering that the upper 5% of individuals are selected based on their phenotypes and allowed to randomly mate *inter se*. The predictions of correlated response were obtained as follows: $CR_Y = ih_x h_y r_a s_{PY}$, where CR is the expected correlated response per generation on trait Y due to direct selection on trait X; i, is the selection intensity; h_x and h_y are the square-root of the heritability for the traits X and Y, respectively; r_a is the genetic correlation between traits X and Y; and s_{PY} is the phenotypic standard deviation for trait Y. The absence of natural selection was assumed to obtain predicted selection response and correlated response.

Results and Discussion

HERITABILITY AND REPEATABILITY ESTIMATES. Heritability estimates are useful to study genetic changes in a breeding population undergoing selection (Falconer, 1989) and to choose the most appropriate among alternative breeding procedures (Cockerham, 1963; Hill, 1971). On the other hand, repeatability estimates are

useful to make predictions of future performance of phenotype from past records as well as to indicate how much can be gained by using repeated measurements and to determine upper limits for the broad or narrow sense heritabilities (Falconer, 1989). In this paper repeatability is discussed as an upper limit of broad sense heritability, when this differs from narrow sense heritability. Date of ripening and fruit development period (FDP) are highly heritable traits, with heritability estimates of 0.94 and 0.91, respectively (Table 2). These heritability estimates are higher than those previously reported (ripening date, 0.79 to 0.89; FDP, 0.73 to 0.98) (Hansche, 1986; Hansche et al., 1972; Monet and Bastard, 1982; Vileila-Morales et al., 1981). This indicates that selection for these traits in either direction should be effective since their phenotypic standard deviations are also high. Nonetheless, those differences are not unexpected since heritability is a function of the population's variability and the environment in which individuals are grown (Cockerham, 1963; Falconer, 1989). It is also function of the experimental design and the statistical procedure used to produce the estimates (Cockerham, 1963; Falconer, 1989; Nyquist, 1991; Searle, 1971). In addition, the extremely high values of heritabilities of both ripe date and FDP found in this study, associated with high heritability estimates (Hansche et al., 1972; Monet and Bastard, 1982; Vileila-Morales et al., 1981) and bimodal and skewed distributions in previous studies (French, 1951; Bailey and Hough, 1959) are indication that both traits may be controlled primarily by a few major genes. Major gene action has been suggested by Hesse (1975) for date of ripening and by Vileila-Morales et al. (1981) for FDP. Neither of these two traits had permanent environment and/or nonadditive genetic effects ($h^2 =$ repeatability). The heritability estimate of 0.78 for date of full bloom is much higher than that of 0.39 reported by Hansche et al. (1972) and significantly lower than that of 0.90 found by Monet and Bastard (1982). Again, due to the nature of heritability estimates these apparent discrepancies should not be unexpected. Like ripe date and FDP, date of full bloom did not show permanent environment and/or nonadditive genetic effects.

Table 2. Narrow-sense heritability, repeatability, phenotypic standard deviation and predicted selection response for 13 peach fruit characteristics evaluated for 3 years at College Station, Texas.

Characters	Heritability	Repeatability	Mean ^a	Phenotypic SD ^a	Predicted selection response ^{z,y,x,w}	
Full bloom (days from 1 Jan.)	0.78	0.78	63.21	8.18	12.92 (20.44)	-14.42 (-22.81)
Ripening (days from 1 Jan.)	0.94	0.94	162.60	27.70	64.52 (39.68)	-35.17 (-21.63)
Fruit development period (days)	0.91	0.91	97.62	33.58	92.74 (95.00)	-30.91 (-31.66)
Fruit mass (g)	0.32	0.51	66.90	22.40	14.20 (21.23)	-12.81 (-19.15)
Soluble solids (%)	0.33	0.52	12.93	2.55	1.72 (13.30)	-1.66 (-12.84)
Titrate acidity ^v (H ⁺ eq/L)	0.31	0.31	7.31	1.63	1.04 (14.23)	
Fruit length ^v (cm)	0.47	0.59	5.04	0.57	0.55 (10.91)	
Fruit suture diameter ^v (cm)	0.38	0.51	4.99	0.29	0.23 (4.61)	
Fruit cheek diameter ^v (cm)	0.31	0.52	4.91	0.54	0.34 (6.92)	
L/W12 ^{v,u}	0.61	0.63	1.02	0.07	0.09 (8.82)	
Fruit blush ^{v,t} (rating)	0.68	0.71	5.42	0.37	3.32 (61.25)	
Fruit tip ^t (rating)	0.45	0.61	7.24	0.67	0.62 (8.56)	-0.68 (-9.39)
Fruit shape ^t (rating)	0.43	0.48	6.55	0.83	0.74 (11.30)	-0.80 (-12.21)

^aValues transformed back to the original scale.

^yAssuming upper 5% individuals are selected and allowed to mate *inter se*. Predicted response per generation.

^xThe column with negative values represents the predicted selection response in the opposite direction.

^wValues inside parenthesis are the predicted selection response in percentage of the population mean.

^vVariables not transformed.

^uRatio of fruit length to average fruit diameter.

^tFruit blush (0 = 0% to 9% red color, 9 = 90% to 100% red color); fruit tip (4 or lower = large and pronounced tip, 9 = no tip); fruit shape (4 or lower = large suture bulge, large and pronounced tip, 9 = round or slightly oblong fruit with no suture or tip).

Fruit blush and L/W12 exhibited moderately high degrees of additive inheritance ($h^2 = 0.68$ and 0.61 , respectively) (Table 2). However, while fruit blush exhibited high variability, L/W12 showed almost no variability. For both traits the contribution of permanent environment plus nonadditive genetic effects was very low. The heritability estimate for fruit blush was three times higher than that previously reported for standard peach (Hansche, 1986) and higher than the estimate of 0.41 cited for dwarf peach (Hansche and Beres, 1980). At least three factors may have contributed to the higher heritability estimate for this trait: 1) larger genetic variability present in the breeding population used in this study, 2) better measurement of the trait (0 to 9 scale used here against 1 to 4 scale used in the previous investigations), and 3) better efficiency of the REML estimator (smaller sampling variances and better use of pedigree information).

Intermediate heritability estimates were found for all of the four measures of fruit size (fruit mass, length, suture, and cheek diameters) (Table 2). With the exception of fruit mass, the other three traits had low phenotypic standard deviations. As a result, selection for fruit size by selecting for one or more of these traits should be more difficult than selecting for fruit mass. The phenotypic standard deviation of 22 g observed for fruit mass, associated with a heritability estimate of 0.32 for this trait, should allow reasonable genetic advance. Previous reports on the inheritance of fruit size have indicated heritability estimates about the same for fruit cheek and a bit lower for length and suture (Hansche et al., 1972), and for fruit mass varying from a little lower (0.26) (Hansche and Beres, 1980) to a considerably higher (0.50 to 0.60) estimate (Hansche, 1986; Monet and Bastard, 1982). The repeatability estimates were 12% to 21% greater than the narrow-sense heritability estimates, and indicate moderate permanent environment and/or nonadditive genetic effects for these traits.

Percent soluble solids ($h^2 = 0.33$) and titratable acidity (TA) ($h^2 = 0.31$) are moderately heritable traits. Acidity also was measured by pH and the heritability ($h^2 = 0.39$) was slightly higher, but the total variability was close to 0 (results not shown). Although an estimated heritability of 0.43 had been reported for percent soluble solids (Monet and Bastard, 1982), this trait and fruit acidity have been considered characters of low heritability ($h^2 \leq 0.19$) (Hansche, 1986; Hansche and Beres, 1980; Hansche et al., 1972). However, as pointed out by Hansche et al. (1972), imprecise measurement of these traits may be one of the causes of the low heritability estimates. In addition to year effects, both traits are affected by maturity stage (Byrne et al., 1991; Firoozabadi and Olmo, 1987; Kader et al., 1982). Percent soluble solids is also affected by canopy location (Marini and Trout, 1984) and water status during the ripening season. Titratable acidity appears to be a good measure of acidity. However, its practical use in breeding is restricted because it cannot be directly used in field determinations. Permanent environment and/or nonadditive genetic effects were not detected for TA, but these parameters responded for 19% of the variation for percent soluble solids. The estimated repeatability for percent soluble solids was 0.52 . Firoozabadi and Olmo (1987) found a relatively high repeatability for percent soluble solids ($r = 0.55$ and $h^2 = 0.34$) and TA ($r = 0.62$ and $h^2 = 0.15$) in grapes. For most traits the repeatability was greater than h^2 (Table 2). Fruit tip and fruit shape had heritability estimates of 0.45 and 0.43 , respectively. Although the phenotypic standard deviations for these traits are not large compared to fruit blush, for example, these heritabilities are sufficiently high to allow acceptable genetic advance. The contribution of permanent environment and/or nonadditive genetic effects for fruit tip (35% of σ_a^2 or 16% of σ_p^2) was greater than the contribution of these effects on fruit shape (10% of σ_a^2 or 4%

of σ_p^2). In fruit trees, these effects are important when selection is based on vegetative reproduction. For example, in peach after a seedling is selected (usually in the F_1), it is grafted and all subsequent evaluations are based on vegetative propagation.

PREDICTED RESPONSE TO SELECTION. Genetic advance is expected to be relatively rapid for date of full bloom, date of ripening, FDP, fruit mass, TA and fruit blush, but not much progress would be expected for most of the other traits (Table 2). One generation of independent selection for early ripening and short FDP would result in quite large gains, 35 d or 22% and 31 d or 32%, respectively. Conversely, one generation of selection for late ripening and long FDP could result in as many as 64 d increase (40%) for ripening time and ≈ 93 d (95%) for FDP. These predicted values indicate that selection for lateness would be $\approx 83\%$ more effective than selection for earliness, and three times more effective for long than for short FDP. The largely skewed distributions is the main cause of this high degree of asymmetry of the selection response observed for both traits, and reinforce the conclusion that major gene effects may be present in both traits (Hesse, 1975; Vileila-Morales et al., 1981), although relationship between the mean and standard deviation also may cause asymmetry. Conversely, this high degree of asymmetry in the predicted selection response also may indicate that there are more genes fixed or toward fixation for both lateness and long FDP than the inverse. The extremely high predicted response toward long FDP is also in part due to the inclusion in the analysis of progeny from 'Gaschina Novembre', a very late cultivar. When those progeny were deleted from the analysis, although the heritability estimates stayed the same, the predicted response was ≈ 20 d shorter (result not shown).

Selection for early bloom should decrease the bloom time by about 14 d (23%) in the first generation of selection. If the interest were in late bloom, which could be desirable to avoid losses due to spring frost in low- and mid-chill areas (Hesse, 1975), the expected gain would be a little lower (13 d). One generation of selection for large fruit size would lead to an increase of $\approx 21\%$ of the population mean fruit mass or ≈ 14.2 g. No significant asymmetry in the response would be expected for this trait. The selection for large fruit size through selection for any of the other fruit size related traits (length, suture, and cheek diameters) would be much less efficient: 5% to 11% versus 21% for average fruit mass. This is because these traits varied less than fruit mass. The predicted values of 1.72 (13%) for percent soluble solids and of 1.04 eq H⁺/L of juice (14%) for TA are stimulating and suggest that both traits are amenable to genetic manipulation. Selection for high or low fruit blush should be highly effective as indicated by the predicted value of 3.3 units (scale 0 to 9), or 61% in the first generation (Table 2). Both the heritability and phenotypic standard deviation found for fruit blush in this breeding population were much higher than those reported for other sources of germplasm (Hansche, 1986; Hansche and Beres, 1980), and this is the reason of such a large predicted response. Naturally, for the second and following generations of selection, this gain is expected to be lower because both the heritability and the phenotypic variance are reduced with selection (Falconer, 1989). On the other hand, with this large predicted response the breeder can be more flexible in selecting for this trait and apply lower selection intensity on fruit blush, and pay more attention to other important characters. Genetic advance for fruit tip and fruit shape should be possible, but slow. Selection for fruit shape should be a little more efficient when this trait is measured by the 0 to 9 subjective scale instead of ratio fruit length to average fruit diameter (L/W12), despite the higher heritability estimate found for the latter. Both fruit tip and shape exhibited intermediate heritabilities but relatively low phenotypic variation,

while L/W12 although it had a higher heritability, its phenotypic variability was much less. The relatively low variability for these traits is not totally unexpected since most parental germplasm used in this study are commercial varieties (many now obsolete) and advanced breeding selections that had been selected for a small tip and a round shape.

It should be noted that selection changes gene frequencies and consequently, the heritabilities of the characters (Hill, 1971; Hansche, 1983; Falconer, 1989). Thus, if only the best performing individuals are selected each generation, the total variability in the population is reduced (Falconer, 1989; Hill, 1971) and as a result, the selection response is also decreased. Hence, the predictions for the traits in discussion are expected to decrease after each additional generation of selection.

GENETIC AND PHENOTYPIC CORRELATION ESTIMATIONS. About 50% of the genetic and one-third of the phenotypic correlations were ≥ 0.30 (Table 3). Date of full bloom was negatively correlated genetically and phenotypically with FDP, but not with date of ripening. These results support the conclusion of Weinberger (1948) that early bloom tends to result in long FDP, but that bloom date is not a reliable predictor of ripening date. It has been pointed out that fruit of a very early blooming cultivar have slow development in the first stage because of cooler temperatures following bloom as compared to a late blooming cultivar (Boonprakob et al., 1992; Sherman and Rodriguez, 1987; Topp and Sherman, 1989a). In fact, high correlations between temperature for various periods following full bloom and FDP have been reported (Boonprakob et al., 1992; Topp and Sherman, 1989a; Weinberger, 1948). The genetic correlation between the two traits found in the present investigation, on the other hand, suggests that there are some genes affecting the relationship between these traits. However, because the response of FDP to temperature is strong (Boonprakob et al., 1992; Sherman and Rodriguez, 1987; Topp and Sherman, 1989a) and because this genotype \times environmental interaction could not be isolated in this study, the genetic contribution to the relationship between bloom date and FDP is probably smaller than suggested by the genetic correlation. There was a negative genetic correlation between date of full bloom and TA, fruit tip, and fruit shape, while a positive genetic correlation was found with L/W12. Early bloom-

ing genotypes tend to have more acidic and better shaped fruit. Since fruit shape is influenced by chilling requirement (Topp and Sherman, 1989b), the negative genetic correlation between bloom date and fruit shape is an indication that many genes that control bloom date and chilling requirement are pleiotropic. Indeed, the association between bloom and chilling requirement have been well documented (Munoz et al., 1986; Sherman and Rodriguez, 1987; Topp and Sherman, 1989a).

Date of ripening and FDP were strongly and positively correlated both genetically and phenotypically, indicating that unlike bloom, FDP is a reliable predictor of ripening date. Both ripening and FDP showed moderately strong positive genetic correlations with percent soluble solids (0.63 and 0.62) and TA (0.55 and 0.64), and strong negative genetic correlations with fruit blush (-0.77 and -0.72). If these genetic correlations are due to pleiotropy only, the development of early ripening cultivars showing high soluble solids content and high fruit acidity may not be possible in this breeding population. On the other hand, the development of early ripening cultivars having fruit with high red blush should not be a problem. The corresponding phenotypic correlations of ripening and FDP with these three traits had the same sign as the genetic correlations but were lower (0.41 and 0.40, 0.32 and 0.37, and -0.57 and -0.55 , respectively). Phenotypic correlations of comparable magnitude between ripening and fruit acidity and ripening and fruit blush were also reported by Hansche et al. (1972). Although moderately weak, the genetic correlations between L/W12 and date of ripening (-0.33) and FDP (-0.46), FDP and fruit cheek and FDP and fruit tip indicate the tendency of early ripening and short FDP genotypes to have smaller fruit size and worse shaped fruit than late ripening genotypes.

Fruit mass and the other three measures of fruit size (length, cheek, and suture diameters) were strongly and positively correlated both genetically and phenotypically. Thus fruit mass is a reliable measure of fruit size. In addition to simplicity of measurement, fruit mass exhibited more variability than any one of the other three traits. Therefore, improvement of fruit size through selection for fruit mass should be most efficient. Fruit mass was also genetically correlated with fruit shape (0.41) and TA (0.37). The genetic correlation of 0.41 between fruit mass and fruit shape

Table 3. Genetic correlations (above diagonal) and phenotypic correlations (below diagonal) among 13 peach fruit characteristics evaluated for 3 years at College Station, Texas.²

Characters ¹	Bloom date	Ripening date	FDP	FW	SS	TA	FL	FS	FC	L/W12	FB	FT	Shape
Bloom date	---	-0.01	<u>-0.33</u>	-0.08	0.05	<u>-0.32</u>	0.18	-0.19	-0.14	<u>0.53</u>	0.11	<u>-0.41</u>	<u>-0.41</u>
Ripening date	0.02	---	<u>0.93</u>	0.21	<u>0.63</u>	<u>0.55</u>	-0.09	0.14	0.22	<u>-0.33</u>	<u>-0.77</u>	0.26	-0.02
FDP	<u>-0.34</u>	<u>0.91</u>	---	0.25	<u>0.62</u>	<u>0.64</u>	-0.13	0.22	<u>0.30</u>	<u>-0.46</u>	<u>-0.72</u>	<u>0.39</u>	0.12
FW	-0.06	0.08	0.11	---	0.26	<u>0.37</u>	<u>0.90</u>	<u>0.99</u>	<u>0.99</u>	-0.19	0.08	0.18	<u>0.41</u>
SS	0.01	<u>0.41</u>	<u>0.40</u>	0.05	---	0.06	-0.04	0.13	0.29	-0.27	<u>-0.56</u>	0.27	0.00
TA	-0.18	<u>0.32</u>	<u>0.37</u>	0.16	<u>0.34</u>	---	-0.05	<u>0.39</u>	<u>0.47</u>	<u>0.57</u>	<u>-0.31</u>	<u>0.37</u>	<u>0.37</u>
FL	0.09	-0.08	-0.10	<u>0.88</u>	-0.07	0.00	---	<u>0.84</u>	<u>0.88</u>	<u>0.57</u>	0.15	<u>-0.51</u>	-0.11
FS	-0.12	0.05	0.10	<u>0.94</u>	0.02	0.15	<u>0.83</u>	---	<u>0.99</u>	-0.18	0.12	0.20	<u>0.49</u>
FC	-0.08	0.08	0.12	<u>0.93</u>	0.05	0.16	<u>0.82</u>	<u>0.91</u>	---	<u>-0.35</u>	0.08	<u>0.33</u>	<u>0.54</u>
L/W12 ³	<u>0.34</u>	-0.25	<u>-0.36</u>	-0.10	-0.18	-0.27	<u>0.35</u>	-0.20	-0.26	---	0.09	<u>-0.83</u>	<u>-0.93</u>
FB	0.08	<u>-0.57</u>	<u>-0.55</u>	0.06	<u>-0.30</u>	-0.17	0.10	0.08	0.06	0.06	---	-0.03	<u>0.31</u>
FT	-0.23	0.16	0.25	0.09	0.15	0.19	-0.26	0.12	0.16	<u>-0.68</u>	-0.03	---	<u>0.81</u>
Shape	-0.24	-0.04	0.06	<u>0.38</u>	0.06	0.21	0.06	<u>0.43</u>	<u>0.43</u>	<u>-0.68</u>	0.17	<u>0.59</u>	---

²Correlation values (r_a or r_p) ≥ 0.65 ; $0.64 \geq r_a$ or $r_p \geq 0.50$; $0.49 \geq r_a$ or $r_p \geq 0.30$; and r_a or $r_p < 0.30$ were considered strong or very strong, moderately strong, moderately weak and weak or very weak, respectively. Correlation values ≥ 0.30 are underlined.

¹FDP = fruit development period, FM = fresh mass, SS = soluble solids, TA = titratable acidity, FL = fruit length, FS = fruit suture diameter, FC = fruit cheek diameter, L/W12 = ratio of fruit length to average fruit diameter, FB = fruit blush, FT = fruit tip, and shape = fruit shape.

³Ratio of fruit length to average fruit diameter.

Table 4. Expected correlated response for fruit characteristics when direct selection is practiced solely for early blooming and early ripening^z.

Characters ^y	Direct response ^x	Early bloom correlated response ^{x,w}	Early ripe correlated response ^{x,w}
Date of full bloom	-14.42	---	0.15
Date of ripening	-35.17	0.42	---
Fruit development period	-30.91	16.64	-29.76
Fruit mass	14.20	1.66	-4.61
Percent soluble solids	1.72	-0.13	-1.76
Titrateable acidity ^v	1.04	0.53	-1.00
Fruit blush ^v	3.32	-0.39	3.01
Fruit tip	0.62	0.35	-0.25
Fruit shape	0.74	0.44	0.03

^zAssuming upper 5% individuals are selected and allowed to mate *inter se*. Predicted response per generation.

^yIn the original scale, date of full bloom and date of ripening are expressed as days from 1 Jan.; fruit development period in days; fruit mass in grams; percent soluble solids in °Brix; titrateable acidity in eq H⁺/L of juice; fruit length, fruit cheek and fruit suture in cm; fruit blush (0 = 0% to 9% red color, 9 = 90% to 100% red color); fruit tip (4 or lower = large and pronounced tip, 9 = no tip); fruit shape (4 or lower = large suture bulge, large and pronounced tip, 9 = round or slightly oblong fruit with no suture or tip).

^xValues transformed back to the original scale.

^wCR_y = ih_yh_xr_as_{py}.

^vVariables not transformed.

although moderately weak, is interesting since it indicates that selection to improve both traits at the same time can be relatively efficient, since opposing responses are not expected to occur. Fruit length showed a moderately strong genetic correlation with L/W12 (0.57) and fruit tip (-0.51), but was not genetically correlated with fruit shape.

Other important relationships were found for percent soluble solids and TA with fruit blush, L/W12 and fruit shape with TA, fruit shape and tip with L/W12, and fruit tip with fruit shape. Percent soluble solids and TA were genetically negatively correlated with fruit blush (-0.56, -0.31), which means that genotypes selected for high red blush will tend to have low TA and low soluble solids content and vice versa. It also means that selection for higher expression of all three characters at the same time may be difficult, unless the estimated genetic correlations are due mostly to linkage disequilibrium. According to Falconer (1989), however, linkage disequilibrium is more likely to occur when crosses are made among cultivars or lines with divergent origins. This does not seem to be the case of the germplasm included in this study, most of which were related. The genetic correlations between TA and both measures of fruit shape indicates that selection for better shape should result in higher acidity. Fruit tip and both measures of fruit shape (L/W12 and FShape) had, as would be expected, strong genetic correlations. The corresponding phenotypic correlations were strong, although not as high as the genetic correlations. Usually, when selection is practiced for fruit shape, fruit with large suture bulges and large and pronounced tips receive the lowest scores, while round or slightly oblong fruit with no suture or tip are given the highest scores. In other words, when selecting for fruit shape the breeder is automatically selecting against fruit tip. Finally, the very strong genetic correlation between the two measures of fruit shape indicates that the use of the subjective scale (0 to 9) is a reliable measure of fruit shape. The greatest advantage of the subjective scale is that it can be used much more easily in the field than the ratio fruit length to average fruit diameter.

Several important genetic correlations (full bloom date with FDP, percent soluble solids with ripe date, FDP with fruit blush, and shape (L/W12), and TA with fruit shape) were in the opposite direction of that desired by the breeder. A positive genetic corre-

lation is not desirable when the character of interest is associated with an undesirable character, or when different degrees of expression of two characters are desired. On the other hand, a negative genetic correlation is not wanted when it involves two desirable characters, such as percent soluble solids and fruit blush. Comstock et al. (1958) pointed out that characters not under selection may deteriorate and those under selection may show little response due to negative genetic correlations. Another result of negative genetic correlations when the two characters have high heritabilities, is that when selection is applied to both characters simultaneously neither responds (Falconer, 1989). In either case, genetic correlations in the contrary direction of that desired contribute to reduce the efficiency of the breeding program (Comstock et al., 1958; Hill and Leath, 1975).

Genetic and phenotypic correlations between date of full bloom, date of ripening, FDP and fruit mass and all six plant traits discussed in the previous paper (Souza et al., 1997) were estimated. Of the 28 possible combinations only one (blind node propensity with full bloom date) had a genetic correlation was greater than 0.30 (results not shown). Since low-chill genotypes bloom earlier than high chill genotypes (Sherman and Rodriguez, 1987), the genetic correlation between blind node propensity and bloom date indicates that high-chill genotypes tend to be more susceptible to blind nodes.

CORRELATED RESPONSE. Four important traits for peaches in low- and mid-chill areas (early blooming, early ripening, short FDP, and large fruit mass) illustrate the importance of correlated response. Selection for early blooming should result in important correlated responses for fruit shape, fruit tip, TA and FDP (Table 4). While one generation of direct selection for early blooming should move the bloom date by nearly 14 d, FDP would be prolonged by ≈17 d or 54% of the direct response. Titrateable acidity should increase ≈0.5 eq H⁺/L of juice (51% of the direct response), while fruit shape and fruit tip should change ≈56% and 59% of the direct response, respectively. Selection only for early bloom should not contribute to earliness of ripening, although ripe date is a function of full bloom date and FDP (Sherman and Rodriguez, 1987; Sherman et al., 1988). Selection practiced solely for either early ripening or short FDP should result in significant effects on most correlated traits. The high correlated response on

FDP due to selection for early ripening and vice versa, indicates that selection either for early ripening or short FDP can be efficiently used to bring forward ripening date. Nevertheless, selection for short FDP should also contribute to lateness of bloom, while selection for early ripening would not affect bloom. The correlated response on fruit blush due to selection for early ripening is expected to be a little higher than that due to selection for short FDP, but in both cases it should be nearly as efficient as the direct selection for this trait. In contrast, selection for early ripening or short FDP should negatively affect fruit mass, percent soluble solids and TA. The negative correlated response on percent soluble solids due to direct selection for early ripening, for example, should be $\approx 6\%$ greater than the direct response against this trait, while that due to direct selection for short FDP should be $\approx 3\%$ greater. Thus, in low-chill areas where the development of early-ripening cultivars is a major goal (Rouse and Sherman, 1989; Sherman and Rodriguez, 1987; Sherman et al., 1988), these undesired correlated responses are an indication that breeders in those areas are likely to be unsuccessful in developing early-ripening and high sugar content cultivars. For TA, the situation is analogous to that of percent soluble solids, but the expected negative correlated response due to selection for short FDP should be $\approx 14\%$ higher than that due to selection for early ripening. For fruit mass, the expected negative effect of direct selection either for early ripening or short FDP should be much lower than that for TA and percent soluble solids, but still of some significance. Fruit shape and date of full bloom would not be affected by selection for early ripening, while a small but positive effect would be observed for fruit tip. Selection for short FDP should also cause small and positive effects on fruit tip and fruit shape.

Selection for higher fruit mass is not expected to cause substantial changes to six of the eight traits considered. However, the effect on ripening and FDP would be relatively important since each 14 g increase in fruit mass would result in a 6- and 7-d increase for ripening date and FDP, respectively. All other correlated traits respond little or not at all (Table 4). Finally, considering that correlated response is a function of the genetic correlation between the characters involved, and that genetic correlation is a function of gene frequency and very sensitive to changes to it (Bohren et al., 1966), caution is needed in the interpretation of the correlated responses discussed above. Genetic correlation, and therefore the correlated response, can change rapidly as a result of selection itself and also due to random genetic drift, the former occurring especially when high selection pressure is imposed in each generation of selection (Falconer, 1989). Furthermore, when both genetic correlations and heritabilities are low, the correlated response is usually inconsistent and of low predictability (Bohren et al., 1966; Falconer, 1989; Hill and Leath, 1975). Therefore, before applying the theory of correlated response in practice, the breeder should be aware that it does not always work as expected.

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