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

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

ABSTRACT. Seedlings of 108 families from crosses among 42 peach [*Prunus persica* (L.) Batsch] cultivars and selections were evaluated for six plant characteristics in 1993, 1994, and 1995. The data were analyzed by using a mixed linear model, with years treated as fixed and additive genotypes as random factors. 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 among traits. The narrow-sense heritability estimates were 0.41, 0.29, 0.48, 0.47, 0.43, and 0.23 for flower density, flowers per node, node density, fruit density, fruit set, and blind node propensity, respectively. Most genetic correlations among pairs of traits were ≥ 0.30 and were, in general, much higher than the corresponding phenotypic correlations. Flower density and flowers per node ($r_a = 0.95$), fruit density and fruit set ($r_a = 0.84$) and flower density and fruit density ($r_a = 0.71$) were the combinations of traits that had the highest genetic correlation estimates. Direct selection practiced solely for flower density (either direction) is expected to have a greater effect on fruit density than direct selection for fruit density.

Knowledge of genetic systems controlling the inheritance of desirable characters, and genetic and environmental factors that influence their expression is fundamental for a successful breeding program (Firoozabady and Olmo, 1987; French, 1951; Kester et al., 1977). The expression of most quantitative traits is complex and is a consequence of a number of segregating loci controlling the trait together with the influence of nongenetic factors. The level of complexity depends on the mode of gene expression and the extent to which nongenetic factors affect individual phenotypes. Hence, each trait may show different patterns of inheritance depending on genetic segregation and the influence of nongenetic factors. The expression of some traits is affected little by the environment (highly heritable traits), while others are greatly affected (low heritable traits). For the latter, it is more difficult to determine the proportion of the phenotypic variation that is due to the genotype. In such cases, multiple year and location evaluations may be required in order to provide a reliable estimate of the genetic value of each individual (Nyquist, 1991).

Although estimates of various genetic and environmental components of variation for quantitative traits have been gathered and usefully applied in a variety of agricultural species (Hesse, 1975), this literature is still limited for fruit and nut crops. In peach, most studies on quantitative traits have been limited to h^2 (narrow-sense heritability) estimation (Hansche, 1986a, 1986b, 1990; Hansche and Boynton, 1986; Hansche et al., 1972; Monet and Bastard, 1982). However, these investigations considered only few traits of commercial importance and only one has examined additive genetic correlations (Vileila-Morales et al., 1981).

Heritability estimates are useful primarily to make predictions

of genetic progress in the offspring when the parents are selected on the basis of their own performance and to choose among the available selection strategies to improve selection efficiency. It also may provide information for examining major changes in the amount and nature of genetic variability over generations (Hansche et al., 1966). Additive genetic correlations are important not only for predicting the level of expression of a character without measuring the character itself, but also for the construction of selection indexes and for a better understanding of gene action (Mode and Robinson, 1959). Genetic correlation between two characters may be due to pleiotropy, although linkage disequilibrium is also a cause of correlation, albeit transitory. The degree of correlation due to pleiotropy expresses the extent with which two characters are controlled by the same genes, but pleiotropic genes do not necessarily cause an observable correlation due to dependence on allele frequencies as well (Mode and Robinson, 1959; Falconer, 1989). The phenotypic correlation is a nonadditive combination of both the genetic and environmental correlations. For characters with low heritabilities, phenotypic correlation is determined mainly by the environmental correlation, whereas for characters with high heritabilities the genetic correlation is more important in determining the phenotypic correlation (Falconer, 1989).

Several plant traits are considered important characteristics in peach production. Flower bud set is important because it indicates the ability to produce large number of flowers and bear a heavy crop under unfavorable conditions (Bailey and French, 1949; Rouse and Sherman, 1989; Weinberger, 1944). High flower bud set and fruit set are desirable peach cultivar characteristics in areas where spring freezes are likely to occur because of the higher probability that sufficient live flower buds and/or fruit will remain to produce a commercial crop (Byrne, 1986; Okie and Werner, 1996; Pérez, 1993; Sherman et al., 1988; Werner et al., 1988). However, these characteristics also increase the cost of fruit thinning, which is a critical factor in early ripening cultivars (Byrne, 1986). Node density also affects flower bud and fruit set

Received for publication 28 Feb. 1997. Accepted for publication 29 Jan. 1998. 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.

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Table 1. Number of genotypes, observations, and Box-Cox transformation coefficients used in variance component and heritability estimation for six peach plant characteristics.

Character	Genotypes (no)	Observations (no.)	Box-Cox transformation coefficients		
			1	K_1	K_2
Flower density	1178	2248	0.44	6.48	6.49
Flowers per node	1178	2248	0.67	1.23	0.55
Node density	1178	2248	-0.71	-88.25	11.24
Fruit density	1178	2253	0.35	4.35	1.91
Fruit set	1176	2211	0.50	10.81	29.05
Blind node propensity	1124	2219	0.42	18.05	32.86

in peach (Blake, 1943). High node density (short internodes) is desirable to reduce tree size and consequently, tree spacing (Hansche, 1983, 1990). Blind nodes, the symptom in which a node has no visual vegetative or reproductive buds (Dorsey, 1935; Blake, 1943), is common in low and medium chill peach production areas (Boonprakob et al., 1994; Richards et al., 1994). Excessive frequency of blind nodes may become an economic problem, especially when cultivars with low flower bud set are grown in areas where spring frost is likely to occur (Byrne, 1986; Werner et al., 1988; Richards et al., 1994; Boonprakob et al., 1994). In this paper we examine the inheritance, genetic and phenotypic correlations and prediction of response to selection of six peach plant characters: flower density, flowers per node, node density, fruit density, fruit set, and blind node propensity.

Materials and Methods

EXPERIMENTAL MATERIALS. The germplasm for this study was mostly yellow, melting flesh peach materials from the Texas A&M Univ., College Station, fresh-market peach breeding program. In total, 108 families from crosses among 42 parents were used. The size of each family varied from a minimum of 4 to a maximum of 15 seedlings. The total number of seedlings evaluated was 1,178 (Table 1). The progeny were 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. Seedlings in both blocks were planted 1.5 m between rows and 0.2 m within rows.

The choice of the crosses (families) was based on 1) availability of seedlings, 2) availability of trees of at least one parent, and 3) at least one of the two parents was included in more than one cross. The seedlings within each cross were sampled at random. However, when the number of seedlings in a cross was no more than 15 (C-90) and no more than 10 (C-91), all of them were sampled. Most parents used were related to each other in some degree, resulting in an overall inbreeding coefficient of the progeny of 0.23.

EVALUATIONS. Seedling evaluations were made in 1993, 1994, and 1995 when they were 3 and 4 years of age. In the C-90, however, blind node propensity was evaluated at 4 and 5 years of age. In each block (C-90 and C-91) seedlings were evaluated for 2 years and all parameter estimates were based on the 2-year data. Flower density, flowers per node and node density were evaluated within 1 week past full bloom for each seedling. The number of flower buds (including opened flowers) and the number of nodes per 20 cm were counted on six randomly sampled 1-year-old shoots. Fruit density and fruit set were evaluated ≈ 30 d after date of full bloom and before fruit thinning. Fruit density, or the number of fruit per 20 cm of shoot, was evaluated using the same procedure described above. Fruit set was defined as the proportion of fruit set per 20 cm to the number of flowers buds per 20 cm, and was

expressed as a percentage. Each character was represented by the average of the six measurements per seedling. Blind node propensity was evaluated once a year early in the spring before full bloom. Five 1-year-old shoots per seedling were randomly chosen, and the total nodes and the number of blind nodes were counted. The results were expressed as a percentage of blind nodes.

STATISTICAL ANALYSIS. The data were transformed according to procedures described by Box and Cox (1964) to establish normality (Table 1). The transformation was of the form $Y' = Y^\lambda$, where λ is a parameter determined from the data. Usually the criterion for determining the appropriate value for λ is to find the value that minimizes the error sum of squares for a given linear regression model. In this study, the value of λ selected was such that the absolute value of skewness of the distribution of the data was minimized. Because the power of the transformation affects the magnitude of the error sum of squares, the following standardized variable that leaves the error sum of squares little affected by the value of λ was used (Box and Cox, 1964):

$$W = K_1 (Y^\lambda - 1) \Rightarrow \lambda \neq 0$$

where

$$K_1 = \frac{1}{\lambda \times K_2^{\lambda-1}}$$

and

$$K_2 = \left(\prod_{i=1}^n Y_i \right)^{1/n}$$

Results for year effects and predicted response to selection were transformed back to the original scale using

$$Y = \exp \left[\frac{1}{\lambda} \ln \left(\frac{W}{K_1} + 1 \right) \right]$$

Additive genetic merit was predicted by the best linear unbiased prediction (BLUP) (Henderson, 1974, 1975, 1977, 1983). BLUP has the great advantage of using pedigree information by incorporating A^{-1} in the mixed model equations (MMEs), where A is the numerator relationship matrix (NRM) containing all relationship information among individuals in the pedigree. In this study, the NRM was constructed based on pedigree information tracing back three generations.

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

The assumptions for this model are

$$E \begin{bmatrix} y \\ u \\ v \\ e \end{bmatrix} = \begin{bmatrix} X\beta \\ 0 \\ 0 \\ 0 \end{bmatrix}$$

and

$$\text{Var} \begin{bmatrix} y \\ u \\ v \\ e \end{bmatrix} = \begin{bmatrix} ZGZ' + B + R & ZG & ZB & R \\ GZ & G & 0 & 0 \\ BZ & 0 & B & 0 \\ R & 0 & 0 & R \end{bmatrix}$$

for $G = A\sigma_a^2$; $B = I\sigma_v^2$; $R = I\sigma_e^2$; and $\sigma_v^2 = \sigma_{na}^2 + \sigma_v^2$

Under these assumptions the mixed model equations (MMEs) are

$$\begin{bmatrix} X'X & X'Z & X'Z \\ Z'X & Z'Z + A^{-1}\lambda_1 & Z'Z \\ Z'X & Z'Z & Z'Z + I\lambda_2 \end{bmatrix} \begin{bmatrix} \beta \\ \bar{u} \\ \bar{v} \end{bmatrix} = \begin{bmatrix} X'y \\ Z'y \\ Z'y \end{bmatrix}$$

where

$$\lambda_1 = \frac{\sigma_e^2}{\sigma_a^2} \text{ and } \lambda_2 = \frac{\sigma_e^2}{\sigma_v^2}$$

Since the variances, i.e., the additive genetic (σ_a^2), the nonadditive + permanent environment (σ_v^2) and the error variances (σ_e^2) were not known, the estimates of the genetic parameters were obtained solving the MMEs iteratively. The variance components were estimated with restricted maximum likelihood (REML), which is a modified maximum likelihood (ML) procedure that accounts for the loss of degrees of freedom due to the estimation of fixed effects (Patterson and Thompson, 1971). The Multiple Trait Derivative-Free Restricted Maximum Likelihood (MTDFREML) computer program was used to estimate the variance and covariance components (Boldman et al., 1993). Variance and covariance components, heritability and repeatability and year effect estimates were obtained simultaneously. The heritability estimated was in the narrow sense (Henderson, 1977, 1983) and the selection unit was individual trees.

A multiple-trait model was used to estimate the genetic and phenotypic covariances (Henderson, 1983), and the analyses were carried out two traits at a time. For each bivariate analysis, estimates of additive genetic, nonadditive + permanent environ-

ment, error (σ_a^2 , σ_v^2 , σ_e^2) and phenotypic ($\sigma_p^2 = \sigma_a^2 + \sigma_v^2 + \sigma_e^2$) variances were obtained for each, as were the covariances between the two traits. The estimates of the variance components from all possible bivariate analyses for each trait were averaged to give the multiple trait model estimates of the variance components. Because the sampling variances of the estimated variance components are not produced by MTDFREML, 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 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 < 0.30 was considered very weak.

Prediction of response to selection was made assuming mass selection and using: $R = ih^2s_p$, 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. Selection response was estimated using the transformed phenotypic standard deviations and were estimated assuming that the upper 5% of individuals are selected as parents based on their phenotypes and allowed to randomly mate *inter se* (Table 2). The absence of natural selection was assumed. Predictions of correlated response were obtained as follows: $CR_Y = ih_x h_y r_a s_{pY}$, where CR_Y is the expected correlated response per generation in 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 traits X and Y, respectively; r_a is the additive genetic correlation between traits X and Y; and s_{pY} is the phenotypic standard deviation for trait Y.

Results and Discussion

HERITABILITY AND REPEATABILITY ESTIMATES. The heritability estimates of node density (0.48), fruit density (0.47), fruit set (0.43), and flower density (0.41) were intermediate values (Table 2). For fruit density, fruit set, and flower density, these heritability estimates were associated with high phenotypic variability, which indicates that genetic change in either direction should not be difficult.

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

Character ^a	Heritability	Repeatability ^b	Mean ^x	Phenotypic SD ^x	Predicted selection response ^{x,w}	
					Positive	Negative
Flower density	0.41	0.47	6.8	3.55	2.95 (43%)	-2.37 (-35%)
Flowers per node	0.29	0.33	0.6	0.28	0.17 (27%)	-0.15 (-24%)
Node density	0.48	0.48	11.1	1.87	1.84 (17%)	-1.43 (-13%)
Fruit density	0.47	0.47	2.0	1.72	1.66 (83%)	-1.08 (-54%)
Fruit set	0.43	0.43	30.7	22.41	19.53 (64%)	-14.74 (-48%)
Blind node propensity	0.23	0.23	34.4	16.81	7.48 (22%)	-6.63 (-19%)

^aIn the original scale, flower density, node density, and fruit density are expressed as number of flower buds, nodes, and fruit per 20 cm of 1-year old shoots, respectively; fruit set as the percentage of fruit to flowers per 20 cm of 1-year old shoots; and blind node propensity as a percentage of blind nodes.

^bRepeatability = $\sigma_a^2 + \sigma_v^2 / \sigma_p^2$; σ_a^2 = additive genetic variance; σ_v^2 = permanent environment + nonadditive genetic variance; σ_p^2 = phenotypic variance.

^xValues transformed back to the original scale.

^wAssuming upper 5% individuals are selected and allowed to mate *inter se*. Predicted response per generation. Percentage of the trait in parentheses.

The heritability estimate of 0.41 for flower density was in close agreement with a 0.38 estimate reported for an analogous trait, amount of bloom (Hansche et al., 1972), but was lower than the heritability values of 0.9 (Pérez, 1992) and 0.55 reported for flower bud set (Rodriguez and Sherman, 1986). The apparent discrepancies among these estimates are not unexpected since heritability is a population specific parameter. In addition, Pérez (1992) did his study in a single year with a small sample size and based the heritability estimate on the regression of selfed families on their parents. Thus, heritability estimates from this procedure are expected to be higher than those from parent-offspring regression with families developed from outcrosses because the covariance between a parent and its selfed progeny is equal to the additive genetic variance (Falconer, 1989; Nyquist, 1991). Rodriguez and Sherman (1986), working with 18-month-old trees that were grown in a denser nursery (50% more than that in this study) also did their study in a single year. Thus, although they stated that their heritability estimate was conservative because selection had been practiced previously, the precision of a single year heritability estimate is usually low, since the precision is a function the total number of observations and genotypes (Falconer, 1989; Nyquist, 1991). In almond, the heritability of flower density was estimated to be 0.54 based on 3 years of data, but single year estimates varied from 0.24 to 0.72 (Dicenta et al., 1993).

Low heritability values were found for flowers per node (0.29) and blind node propensity (0.23). However, these heritability values are sufficiently high to allow acceptable levels of genetic progress for several generations. For example, for flowers per node where the desirable mean is probably between 1 and 2 flowers per node, three generations of selection on the upper 5% of individuals should move the average from 0.6 (Table 2) to 1.1 flowers per node. The number of flowers per node is a function of flower density and node density and so, by selecting for either high flower density or low node density one can also increase the number of flowers per node indirectly (assuming no undesirable genetic correlation between these traits). Pérez (1992) reported heritability estimates of 0.98 (based on 11 families originated from selfing) and 0.45 (based on 10 families of F_1 hybrids) for blind node propensity, which are much higher than the heritability of 0.23 obtained in this study. Smith and Kinman (1965) have shown that the correct estimator of h^2 by parent-offspring regression is $b/2r_{xy}$, where b is the slope of the regression and r_{xy} is the coefficient of relationship between parent and offspring. In Pérez's study, r_{xy} should be 1 (parents were selfed to give their offspring) or close to it, and this may explain the large difference between his two estimates.

The repeatability being almost equal to heritability estimates

indicate that the effects of nonadditive genetic merit and permanent environment were of minor importance for all six traits (Table 2). In a study of the number of flowers and fruit per seedling, Hansche (1986b) found that $\approx 50\%$ of the total genetic variation for number of flowers per seedling was due to nonadditive gene action, but no nonadditive gene effects were found for number of fruit per seedling. Hansche (1986b) measured both traits using scores rather than the actual number of flowers or fruit. The absence of gene effects other than those due to additive effects influencing these six plant characters is an important result since simple selection procedures can be used to improve these traits.

PREDICTED SELECTION RESPONSE. Selection of the best 5% of the population as parents should lead to relatively rapid genetic progress for most traits (Table 2). Selection for high flower density should result in an increase of 2.9 flowers/20 cm of shoot or 43% of the mean in the first generation of selection. One generation of selection for high fruit density and high fruit set should produce an increase of 83% or 1.6 fruit/20 cm of shoot and increase the ratio of fruit to flowers by ≈ 19.5 percentage units, or 64% in relation to the mean fruit set. The average fruit density was 2 fruit/20 cm of shoot, somewhat higher than the 1.3 fruit/20 cm required for a full crop (Byrne, 1986). However, the predicted selection response indicates that the potential for increasing fruit density is high. This should be also true for the percentage of fruit set. On the other hand, one generation of selection in the opposite direction for low flower and fruit densities would cause a decrease of 2.4 flowers/20 cm or 35% (compare 43% with positive selection) and 1.1 fruit/20 cm or 54% (compare 83% with positive selection), respectively. Fruit set would decrease by 48% with selection for reduced fruit set versus a 64% increase with selection for increased fruit set. This asymmetry in response is expected as the distributions of phenotypes are skewed. Larger responses occur in the direction of the skewness, and the greater the degree of skewness the greater the asymmetry of response. Thus, these results demonstrate the importance of the assumption of normality in quantitative genetic analysis, which is generally assumed but rarely verified. Asymmetrical responses can also occur with divergent selection due to natural selection, random genetic drift, inbreeding depression, genetic asymmetry, maternal effects, and genes with major effects (Falconer, 1989).

The predicted response for flowers per node indicates that one generation of selection for this trait would lead to an increase of $\approx 27\%$ of the mean or 0.17 flowers/node. No significant asymmetry in response would be expected for this trait. On the other hand, because the number of flowers per node is a function of flower and node densities, the effect of indirect selection on this trait may be of more interest than direct response, since breeders interested in this trait are more likely to practice selection for either low or high

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

Character ³	Flower density	Flowers/node	Node density	Fruit density	Fruit set	Blind node propensity
Flower density	---	<u>0.95</u>	<u>0.65</u>	<u>0.71</u>	-0.20	0.08
Flowers per node	<u>0.93</u>	---	<u>0.35</u>	<u>0.60</u>	-0.24	-0.29
Node density	<u>0.31</u>	-0.04	---	<u>0.45</u>	0.09	<u>0.69</u>
Fruit density	<u>0.47</u>	<u>0.40</u>	0.21	---	<u>0.84</u>	0.26
Fruit set	0.24	-0.26	0.05	<u>0.71</u>	---	<u>0.38</u>
Blind node propensity	-0.12	-0.25	<u>0.30</u>	0.01	0.09	---

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 very strong, moderately strong; moderately weak and very weak, respectively. Correlation values ≥ 0.30 are underlined.

³Flower density, node density, and fruit density are expressed as the number of flower buds, nodes, and fruit per 20 cm of 1-year old shoots, respectively; fruit set as the percentage of fruits to flowers per 20 cm of 1-year old shoots; and blind node propensity as a percentage of blind nodes.

Table 4. Expected correlated response for plant characteristics when direct selection is practiced solely for flower density and fruit density^a.

	Flower density correlated response ^{x,w}	Fruit density correlated response ^{x,w}
Flower density	---	2.19 (-1.85)
Flowers per node	0.19 (-0.16)	0.12 (-0.11)
Node density	1.05 (-0.91)	0.76 (-0.68)
Fruit density	1.03 (-0.77)	---
Fruit set	-3.26 (3.45)	16.91 (-13.21)
Blind node propensity	0.75 (-0.76)	1.29 (-1.26)

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

^xIn the original scale, flower density, node density and fruit density are expressed as number of flower buds, nodes and fruits per 20 cm of 1-year old shoots, respectively; fruit set as the percentage of fruits to flowers per 20 cm of one-year old shoots; blind node propensity as a percentage of blind nodes.

^xCR_y = $i h_x h_y r_a s_{py}$

^wValues inside parentheses are the predicted correlated response in the opposite direction.

flower density or for short or long internodes (Werner et al., 1988). Node density had the lowest predicted selection response of 16% of the mean per generation. For selection against blind node propensity, the expected genetic gain of 6.6% or $\approx 19\%$ of the mean per generation is promising.

GENETIC AND PHENOTYPIC CORRELATION ESTIMATES. About two-thirds of the estimated genetic and 43% of the phenotypic correlations were ≥ 0.30 (underlined in Table 3). Most of the genetic correlations were much higher than the corresponding phenotypic correlations. This is expected, in part, because the heritabilities were in the low to intermediate range (Table 2), which indicates the importance of environmental contributions to the phenotypic variation (Searle, 1961). In these cases, the phenotypic correlations are determined by the environmental contribution to the total variation in each trait and to the environmental correlation. A phenotypic correlation that is lower than the genetic correlation does not imply that a negative environmental correlation is involved. A negative environmental correlation is implied only when the ratio of the phenotypic correlation to the genetic correlation is less than the geometric mean of the heritabilities for the two traits (Searle, 1961).

Flower density and flowers per node were positively and strongly correlated both genetically and phenotypically (0.95 and 0.93 respectively). The very strong positive genetic correlation between flower density and flowers per node suggests that these two traits are largely controlled by the same genes. Flower density also had strong positive genetic correlations with fruit density (0.71) and node density (0.65), indicating that increasing the number of nodes/20 cm, results in an increase in the number of flowers and fruit/20 cm. The strong genetic correlation between flower and node densities supports the findings of Blake (1943) that short internodes in standard peaches (not dwarf) are associated with a heavy flower bud set. The corresponding phenotypic correlations among these three traits were also positive, but of much lower magnitude. The moderately strong and positive genetic correlation between flowers per node and fruit density (0.60) also reveals that the expression of these two traits should increase or decrease together. The genetic correlation between flowers per node and node density was positive and moderately weak (0.35), but there was effectively no phenotypic correlation.

Node density and blind node propensity had a genetic correlation greater than twice the phenotypic correlation (0.69 vs. 0.30).

The low heritability of blind node propensity is probably the major determinant of this large difference between the two correlations (Searle, 1961). Node density was also moderately genetically correlated with fruit density (0.45), but not with fruit set, which was strongly and positively correlated genetically and phenotypically with fruit density (0.84 and 0.71, respectively). Fruit set had a moderately weak positive genetic correlation (0.38) with blind node propensity.

CORRELATED RESPONSE. Direct selection for high flower density would result in a positive correlated responses for flowers per node of $\approx 12\%$ and 7% greater than direct selection in the first generation of selection for positive and negative selection respectively (Table 4). Thus, selection for flower density is a more efficient approach to select for flowers per node than is direct selection for flowers per node. In fact, flower density had greater phenotypic variability, higher heritability and, consequently, higher predicted selection response than flowers per node. For all other traits, however, the correlated response is smaller than the direct response, varying from 10% to 62% of the direct response. However, no important undesirable correlated responses are expected. Also, it is interesting that for most traits the skewness in the data is such that both direct and indirect selection should be more efficient when practiced in the positive than in the negative direction.

Indirect selection, or selection for a secondary trait to obtain a correlated response in a commercially important trait, cannot be expected to be better than direct selection unless the secondary character is highly heritable and the genetic correlation is high. However, there are practical situations in which indirect selection may be preferred, for example, when the character is expensive or difficult to measure with precision (Searle, 1965) or when the assessment of the secondary character allows selection earlier in the life cycle (Falconer, 1989). However, the most effective use of a correlated character is in combination with the desired character, as an additional source of information about the breeding values of individuals (Falconer, 1989).

Peach breeders in a medium chill zone can use the heritability and phenotypic standard deviation estimates to help them choose which traits are more susceptible to selection, or to decide which selection intensity should be applied to give an acceptable genetic progress per generation. For example, flower and fruit densities and fruit set are easier to select for than flowers per node, node density or blind node propensity. However, all six traits studied are susceptible to genetic advance. The repeatability estimates, on the other hand, indicate that mass selection is an efficient procedure to improve the traits under study because nonadditive genetic effects are not involved. They also give breeders an idea of how the selected genotypes may perform through the years. The genetic and phenotypic correlation estimates and the predicted correlated responses indicate that the breeder can use direct selection for either flower or fruit densities and obtain desirable indirect responses for all five traits under selection, except blind node propensity. If breeders' preference is for independent selection for each trait, the genetic correlation estimates can be used to help them decide which selection intensity should be applied for each trait to avoid or minimize the effects of undesirable correlated responses, especially for blind node propensity. The susceptibility of the medium chill zone of the southeastern United States (Byrne, 1986; Okie and Werner, 1996) to spring frosts increases the relevance of traits such as flower and fruit densities, flowers per node and fruit set in the selection and development of new cultivars, and breeders must decide whether positive selection for these traits is advantageous compared to the increase in cost of fruit thinning if frost does not occur.

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