

Inheritance of Fruit Size, Soluble Solids, and Ripening Date in *Prunus domestica* cv. Agen¹

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Abstract. Genetic and environmental components of variance were estimated in 2 seedling populations of plum and prune at the University of California, Davis, California; the first population comprised 90 progeny of 14 open-pollinated parents, the second, 430 progeny of 50 controlled crosses among 28 parents. The estimates of phenotypic and genotypic variability associated with these traits in these 2 populations were nearly identical. Heritabilities, estimated by regressing the 500 progeny from the second population on their 50 mid-parents, were very high (0.80–1.0) for fruit size measurements and ripening dates, but zero for fruit yield. Also high (0.49) was the maximum heritability of percent soluble solids, estimated by the genetic variance/phenotypic variance. Phenotypic correlations among the traits fruit size, ripening date, and percent soluble solids are also small but significant in this seedling population. These results indicated that the rates of gain to be expected from mass selection on such populations are substantial.

Breeding stocks with high heritabilities can be improved by simple and relatively inexpensive "mass-selection" methods. Expensive and time-consuming progeny tests are unnecessary because superior genotypes (potential parents) can be discriminated from inferior genotypes in segregating populations by direct measurements of performance. With high heritability, the breeder is also free to allow selected parents to mate randomly, *inter se*, and need not resort to the expensive techniques of positive and negative assortative matings that are required when overdominance and epistasis have important effects on performance (2).

Recent studies of the inheritance of several quantitative traits in breeding stocks of *Prunus avium* L. (sweet cherry) and *P. persica* L. (peach), close relatives of *P. domestica* cv. Agen (plum and prune), indicate that several traits of major commercial importance have heritabilities high enough to ensure relatively rapid improvement of breeding stocks via direct mass-selection breeding methods. In a sweet cherry breeding stock, for example, heritability has been shown (3) to be 0.88 for fruit ripening date, and 0.47 for fruit diameter and for fruit firmness. In a peach breeding stock, the heritabilities were 0.84 for fruit ripening date and 0.31 for fruit diameter (4). If only the best 10% of potential parents were selected for these traits the expected rates of improvement per generation in sweet cherry would be 45% for fruit ripening date and 22% for both fruit diameter and fruit firmness. The rate of improvement of peach breeding stocks would be 6% for fruit diameter (consequently about 18% for fruit volume) and 17% for fruit ripening date.

This study was done to ascertain whether homologous traits in *P. domestica* cv. Agen could be effectively and efficiently improved by direct mass-selection methods. Estimates of several parameters were established: 1) the magnitude of phenotypic, genotypic, and environmental variability of several commercially important traits in *P. domestica* cv. Agen breeding stocks at U.C.D.; 2) the heritabilities of these traits; 3) the rates of genetic improvement expectable from mass selection; and 4) the correlations among commercially important traits that might interfere with genetic improvement.

Materials and Methods

Estimates of variance components were obtained from 3 populations. The first population, grown in the U.C.D. orchard at Davis, CA, consisted of the progeny of 14 open-pollinated parents. Measurements of fruit ripening date and of several characteristics of 10 fruit samples were obtained from each of 90 random 5-year-old seedlings in this orchard in 1973; and measurements were made of fruit ripening date and of several characteristics of two 10-fruit samples from each of the same 90 seedlings in 1974.

The linear statistical model from which these data provided least-squares estimates of the year effects, estimates of the variance among seedlings, V_{as} , and variance within seedlings, V_{ws} , and the variance attributable to seedling-year interactions, $V_{s,y}$, is:

$$x_{ijk} = \mu + s_i + y_j + s.y_{ij} + ws_{ijk}$$

where $i = 1, 2, \dots, 90$; $j = 1, 2$; $k = 1$ in 1973 and $k = 1, 2$ in 1974. In this model x_{ijk} stands for the k^{th} observation of the i^{th} seedling in the j^{th} year. The effects in the model on the x_{ijk}^{th} measurement stand for an overall mean, μ , a random effect contributed by seedling (genotype), s_i , a fixed effect contributed by year y_j , a random effect attributed to interaction of genotype i with year j , $s.y_{ij}$, and a random effect of the k^{th} sample from the i^{th} seedling in 1974.

The second population studied, grown in a U.C.D. orchard 10 miles from Davis, CA, consisted of approximately 430 seedlings from 50 crosses made between 1945 and 1960 among 28 parents.

Measurements of bloom date, fruit ripening date, and several characteristics of 10 fruit samples were obtained from each of these seedlings during the first year they came into bearing. The total variance of these measurements was taken as the phenotypic variance, V_p , of this population. Heritability estimates were obtained from the linear regression of the average performance of offspring, during their first year of bearing, on the mean performance of their parents (1).

The third population consisted of a random sample of 50 nine-year-old trees of the cv. Agen grown on *P. cerasifera* Ehr. rootstocks in a commercial orchard located 8 miles from Davis, CA. A sample of 10 fruits/tree was collected from each of these trees in 1973 and in 1974.

The linear statistical model from which these data provided estimates of the variance among clones of identical genotype, V_{ac} , is:

$$x_{ij} = \mu + c_i + y_j e_{ij}$$

where μ is the overall mean, c_i is a random effect contributed by clone i ; y_j is a fixed effect attributed to year j ; and e_{ij} is a random effect associated with the measurement of the i^{th} clone in the j^{th} year.

Measurements. Dates of full bloom and fruit ripening were measured in number of days from February 18 and July 1, respectively. Crop was estimated subjectively by arbitrarily scoring the fruit from a tree on a scale of 1 to 7, from a very light crop to a good commercial crop. Fruit length, cheek and suture diameters, and fruit pit length are given in millimeters and wt of fruits in g. Percent soluble solids was obtained from a slurry of 10 homogenized fruit halves.

Results

Two seedling populations of *P. domestica* at U.C.D. were used for estimating phenotypic and genotypic contributions to variability among several traits.

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Table 1. Estimates of the mean and of variance components of measurements of several traits of a seedling population of *Prunus domestica* observed in 1973 and 1974. $R.I. = V_g/(V_{as} + V_{s,y} + V_{ws})$ is an estimate of the relative importance of genes in determining the expression of these traits.

Trait	\bar{x}	V_{as}	V_{ac}^y	V_g	$V_{s,y}$	V_{ws}	R.I.
Fr. length	53.8 mm	45.7	2.2	43.5	1.9	1.2	.89
Fr. width	41.7 mm	23.9	1.0	22.9	.9	1.0	.89
Fr. suture	45.5 mm	20.4	.7	19.7	1.0	.8	.89
Fr. wt	55.1 gm	282.0	6.6	275.4	13.0	7.5	.91
Pit length	29.0 mm	11.0	.9	10.1	.7	.3	.84
Sol. solids	20.6%	9.1	3.5	5.6	1.4	.9	.49

^z The degrees of freedom available for estimating these variance components were as follows: V_{as} , 89; V_{ac} , 49; $V_{s,y}$, 89; and V_{ws} , 89.

^y These estimates of the variance among clones of a single genotype were obtained from a local commercial orchard.

The progeny of 14 open-pollinated parents were measured in 1973 and 1974. These measurements were adjusted for the average effects of change in climate between 1973 and 1974, eliminating the effects of climate change from the variation analyzed here (see Materials and Methods). From those data we calculated the single fruit means, \bar{x} , the variance of 10 fruit samples taken within the same seedlings, V_{ws} , the variance among seedlings, V_{as} , and the variance arising from interaction of the seedlings with the climatic difference between 1973 and 1974, $V_{s,y}$ (Table 1).

The sum of these estimated variance components, $V_{as} + V_{s,y} + V_{ws}$, of course represents the phenotypic variance, V_p , of 10 fruit samples in this seedling population. $V_{s,y}$ and V_{ws} are attributable entirely to environment, while V_{as} is attributable in part to the seedlings being of different genotype, and in part to the environmental differences within the seedling orchard. The portion of V_{as} attributable to the genotypic differences could not be determined directly since there was no direct way of estimating how much of V_{as} was attributable to environmental differences in the seedling orchard. The magnitude of effects of environmental differences in this seedling orchard could be estimated indirectly, however, if it is reasonable to assume that these effects are equal to those in a nearby local commercial prune orchard. We made this assumption and took the variance of measurements among the clones, V_{as} , in the commercial orchard as an estimate of that portion of V_{as} attributable to

environmental differences in the seedling orchard (Table 1). Subtracting V_{ac} from V_{as} then gave an estimate of the variance attributable to genes, V_g , i.e., $V_g = V_{as} - V_{ac}$ (Table 1).

The relative importance of genes, R.I., in determining the expression of these traits in this seedling population was taken to be V_g/V_p (2). Apparently, about 90% of the variance in fruit size and seed size is attributable to genetic differences among seedlings, while about one-half of the variance in soluble solids is attributable to genetic differences (Table 1).

The second set of measurements analyzed was taken between 1948 and 1966 on 430 seedlings during the first year they came into bearing at U.C.D. These seedlings were the progeny of 50 controlled crosses made among 28 different genotypes. Those data yielded estimates of the phenotypic variances, V_p , of fruit length, width, suture and wt in this population (Table 2). The portion of V_p , attributable to segregating genes, V_g , was estimated by subtracting from V_p the previously estimated contributions of environment to the variability of these traits (Table 1). That is, V_g was taken to be equal to V_p minus $V_{s,y}$ minus V_{ws} (obtained from the first population of seedlings analyzed) minus V_{ac} (obtained from the local commercial orchard): $V_g = V_p - V_{s,y} - V_{ws} - V_{ac}$.

The relative importance of genes in determining the expression of fruit size in this population was again taken to be $R.I. = V_g/V_p$ (Table 2). Notice that our estimates of the relative importance of genes in determining fruit size are nearly identical for the 2 populations. That is not surprising, since the seedling populations analyzed represent sequential generations in our breeding stock (the parents of the first seedling population analyzed were seedlings from the second population analyzed).

The heritabilities of full bloom, ripening date, fruit size, and yield in this second seedling population were estimated by regressing offspring performance on that of their mid-parent (Table 3). These heritability estimates are consistent with our independent estimates of the relative importance of genes (R.I., Tables 1 and 2) in determining the expression of fruit size in these populations. Furthermore, they indicate that almost all the genetically induced variability estimated

Table 2. Estimates of the phenotypic, genotypic, and environmental components of variance of fruit size in a population of 430 *Prunus domestica* seedlings measured between 1946 and 1965 during their first year of bearing. $R.I. = V_g/V_p$.

Trait	V_p	V_e^z	V_g	R.I.
Fr. length	45.3	5.3	40.1	.88
Fr. width	24.1	2.9	21.2	.88
Fr. suture	24.0	2.6	21.4	.89
Fr. weight	206.0	27.2	178.8	.87

^z $V_e = V_{s,y} + V_{ws} + V_{ac}$.

Table 3. Heritabilities, h^2 , and expected rates of gain, R, in the breeding stock mean, \bar{x}_{bs} , resulting from selecting as parents the upper 20% of seedlings of the U.C.D. breeding stock. The selection coefficient, S, of each trait is equal to 1.4 times the phenotypic standard deviation of the trait.

Trait	$h^2 \pm S.E.$	\bar{x}_{bs}	\bar{x}_{sp}^z	S	R	$(R/\bar{x}_{bs}) \times 100^y$
Blm dt	.86 \pm .19	28.5	17.0	11.5	9.9 days	35%
Ripe dt	.84 \pm .05	44.3	14.3	30.0	25.2 days	57%
Yield	-.17 \pm .21	6.3	9.1	2.8	0	0
Fr. length	1.00 \pm .07	47.4	56.8	9.4	9.4 mm	17%
Fr. width	.79 \pm .06	38.6	45.5	6.9	5.5 mm	14%
Fr. suture	.85 \pm .07	38.1	45.0	6.9	5.9 mm	15%
Fr. wt	.97 \pm .07	37.3	57.4	20.1	19.5 gm	52%
Sol. solids*	.49	20.6	25.3	4.7	2.3%	9%

^z Mean of selected parents.

^y Selection response in percent of the breeding stock mean.

* Computed on the basis of V_g/V_p being a maximum estimate of h^2 .

by V_g in these 2 populations (Tables 1 and 2) is attributable to genes that have additive statistical effects on phenotype. In fact, they indicate that 90% of the total variability associated with full bloom, ripening date, and fruit size in these seedling populations is attributable to genes with additive statistical effects.

The heritability of yield, -0.17 ± 0.21 , was a conspicuous exception on 2 counts: 1) its estimated heritability was not significantly different from zero, whereas the heritabilities of the other traits were near one; and 2) subjective measurement of this trait is known to be open to far greater error than the objective measures used for the other traits (3 and 4). It thus remains unknown whether or not any real differences in yields of seedling trees during their first year of bearing were due to genes with additive effects. All that these results indicated was that the subjective measure of yield we used was not precise enough to discriminate whatever genetic differences in yield there may be among these seedlings.

The potential rates of genetic improvement of these breeding stocks can be estimated from the relationship $R = h^2S$, where S is the selection differential and R is the response per generation (2). Assume that only 20% of the seedlings are selected on the basis of superior performance and are allowed to mate randomly, *inter se*. Then the expected response of their progeny is as given in Table 3. These estimates indicate that mass selection could cause large per-generation responses in fruit size and ripening date and a moderate response in percent soluble solids.

When correlations among these traits are large, responses to selection are also expected to be correlated, enhancing or impeding genetic improvement when selection is practiced on 2 or more traits. We found the phenotypic correlation between ripe date and fruit wt to be .22, between ripe date and % soluble solids to be .22 and between fruit wt and percent soluble solids to be -.13. (The 95% confidence intervals for those estimates, computed via Fisher's Z statistic are all $\pm .11$.) All of these correlations are significantly different from zero

with 95% confidence. They are small, however, suggesting that selection would not be affected greatly by basing selection on multiple traits.

Conclusions

This analysis gives results comparable to those obtained with *P. avium* L. (sweet cherry) and *P. persica* L. (peach) (3, 4). In each of those species, expression of date of bloom, date of fruit ripening, and fruit size are largely controlled by genes, whereas percent soluble solids is under slightly less genetic control. Further, heritability estimates indicate that the genes that control full-bloom date, ripening date, and fruit size are almost entirely additive in effects. The statistical properties of genes controlling percent soluble solids have yet to be determined. Finally, no large adverse correlations appear to exist among traits of ripening date, fruit size, and percent soluble solids in these populations. Consequently, we concluded that inter-mating of parents selected on the basis of their own performance could be very effective and efficient in improving the genetic potential of such breeding stocks in bloom date, ripening date, fruit size, and probably (though not certainly) soluble solids.

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Stress Ethylene Production in Apple Shoots¹

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Abstract. Increases in internal ethylene concentrations occurred after attached and detached apple (*Malus domestica*, Borkh. cv. Winesap) shoots were placed in a horizontal position. Ethylene was higher in the underside of the shoot, and decreased linearly in a basipetal direction along the axis. Bent and horizontally-oriented detached shoots did not increase in ethylene at 20°C, but increased to identical levels at 30°, suggesting that responses to the 2 types of stress were identical. Although gravitational stress alone increased ethylene levels, an experiment designed to separate bending stress from gravitational stress was inconclusive because rotation decreased shoot ethylene levels.

Tying stems into arcs increased internal ethylene levels as much as 10-fold (11, 23), but it was not determined if the ethylene increase resulted from physical bending stress or from gravitational stress caused by stem reorientation. Horizontal positioning of apple stems (7, 25, 26) has long been known to decrease growth and increase flower production. Gravitational stress has also been reported to influence flowering of such unrelated plants as pineapple (21) and soybean (5). Flowering is regulated in pineapple by ethylene (4, 24). Coleus plants placed in a horizontal position produced more ethylene with a subsequent enhancement of leaf abscission (2). Pretreatment of erect sunflower plants with ethylene or horizontal orientation inhib-

ited polar transport of ¹⁴C-IAA and induced similar characteristic symptoms, suggesting that effects of horizontal orientation might result from a stimulation of ethylene production (22). In this study we examined ethylene levels and distribution in horizontally positioned apple shoots.

Materials and Methods

Experiments were conducted in July and August, 1972, using vigorous new vertical shoots, both attached and detached, from the tops of mature apple trees at the Purdue University Farm. Unless otherwise designated, similar shoots 100 cm long and 1 cm thick at the base were used, and ethylene was obtained from a 10 cm section taken 45 cm away from the shoot tip. Each experimental replicate contained 4 shoots.

As illustrated in Fig. 1, the term "horizontal shoot" denotes shoots

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