

Heritabilities of Seedling Traits in a *Prunus domestica* (L.) Breeding Population

C. DeBuse, D.V. Shaw and T. DeJong
Department of Pomology, University of California
Davis, CA
USA

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Abstract

Heritabilities of seedling growth traits were assessed in a California prune breeding population. A partial diallel design was created with 17 controlled crosses, using 18 parental trees within the UC Davis *Prunus domestica* elite breeding germplasm. The seedlings were grown in a greenhouse for two months followed by an additional eight months in an outdoor nursery planting. Trunk radius, tree height, combined branch and trunk length were measured and growth index ((radius)² * height) was calculated after two months in the greenhouse. Trunk radius, tree height, tree fresh weight were measured and growth index ((radius)² * height) was calculated after a subsequent eight months in a field nursery. Data for all traits were analyzed using restricted maximum likelihood (REML) to obtain estimates of genetic and environmental variances and these variances were used to calculate narrow-sense (h^2) and broad-sense (H^2) heritabilities. Heritabilities differed substantially among traits and over time. Heritabilities for two-month measurements were $h^2 = 0.23-0.47$ and $H^2 = 0.44-0.60$, whereas heritabilities for traits measured after eight months in the field were $h^2 = 0.08-0.27$ and $H^2 = 0.13-0.27$. The utility of these heritability estimates for designing optimal selection strategies depends on the relationship between seedling growth characteristics and traits of commercial importance, and on the consistency of trait expression at different life-cycle stages.

INTRODUCTION

Breeding a new *Prunus domestica* (European plum) cultivar can be a time consuming and expensive process. A large number of offsprings from controlled crosses are required at the initiation of each selection cycle, and then over several years the non-productive or undesirable seedlings are eliminated, with only a few elite seedlings remaining in the residual population. The elimination of seedlings with lower potential early in the process may reduce the time needed to develop a cultivar and conserve resources for other breeding tasks. Seedling growth characteristics could be used to select vigorous and strong mature trees if the traits measured the first year are genetically correlated to commercially important characteristics of the mature tree. High heritabilities of the traits could make it possible to increase the genetic gain over each generation with selection at this growth stage (Searle, 1965).

Heritability and genetic correlation can be useful breeding tools in many different species (Burdon, 1977; Lipow and Wyatt, 1999; Shaw et al., 1988; Shaw, 1993). Muranty et al. (1998) demonstrated that moderate to high heritabilities for growth traits in wild cherries, height and girth, could be used to select more vigorous trees at an early age. In strawberries, large genetic effects and strong correlations were found for vegetative growth traits and productivity. The correlation between vegetative growth and reproductive patterns indicated that it may be possible to improve yield by selecting for certain vegetative characteristics (Shaw, 1993).

Correlation of traits at early and later lifecycle stages have been studied in forestry breeding programs in the hopes that early culling could eliminate unwanted characteristics found in later lifecycle stages. Studies on loblolly pine seedling traits have shown a positive correlation between seedling height and five-year height, but that seed

characteristics and trunk diameter showed no similar correlation (Robinson et al., 1984). Conversely, Namkoong and Conkle (1975) reported that Ponderosa pine families that were rated the tallest after three years of growth were not the tallest after 20-29 years of growth. These studies indicate that the relationship between early and late lifecycle stages is not predictable a priori, and that species may differ in this regard.

We examined the seedling growth characteristics and their narrow-sense and broad-sense heritabilities and genetic correlation in a California *P. domestica* breeding population to assess the potential for using seedling characteristics in early selection.

MATERIALS AND METHODS

A partial diallel design was created with 17 controlled crosses, using 18 parental trees within the UC Davis *Prunus domestica* elite breeding germplasm. The controlled pollinations were performed, in the spring of 2001, at the Kearney Agricultural Center, in Parlier, California. After stratification (February, 2002), the seedlings were planted in a naturally-lighted greenhouse arranged in a randomized complete block design with four blocks. Each block contained nearly equal numbers of offspring from each cross, arranged in noncontiguous plots (Libby and Cockerman, 1980). Measurements of seedling height, trunk diameter at soil level, and branch lengths were recorded two months after germination. These measurements were combined to form four variables for further analysis: a) two-month radius (diameter/2), b) two-month height, c) combined branch and trunk length, and d) two-month growth index ((radius)² * height).

The seedlings were moved from the greenhouse after two months (May, 2002) and planted in an outdoor nursery, near Newcastle, California; and grown under commercial nursery conditions at a spacing of 12-14 inches for the remainder of the growing season. The experimental design for the nursery was unchanged from the greenhouse. After the seedlings reached full dormancy, they were undercut, washed and stored in a covered sawdust bed. Individual trees were measured for height, diameter of the trunk just above the soil line, and total fresh weight. These measurements were combined to create four variables: a) ten-month radius (diameter/2), b) ten-month height, c) ten-month fresh weight, and d) ten-month growth index ((radius)² * height).

The values of the measurements were examined for scale effects on variance components by using Fernandez's (1992) method. Regression of the natural log of the mean on the natural log of the standard of deviation was performed for each variable prior to statistical analysis. These regressions were significant for four variables, and power transformations were applied to the values for two-month radius, two-month growth index, combined branch and trunk length, and ten-month radius.

All variables were analyzed using the restricted maximum likelihood (REML) method of Huber et al. (1992) to develop estimates of variance for General Combining Ability (σ^2_{GCA}), Specific Combining Ability (σ^2_{SCA}), and variance within full-sib families (σ^2_w), from which genetic and environmental variances were calculated. Narrow-sense and broad-sense heritabilities were calculated using the following equations (Hallauer and Miranda, 1981).

$$\begin{aligned} \sigma^2_A &= 4(\sigma^2_{GCA}) \quad , \\ \sigma^2_D &= 4(\sigma^2_{SCA}) \quad , \\ h^2 &= \frac{4(\sigma^2_{GCA})}{2(\sigma^2_{GCA}) + \sigma^2_{SCA} + \sigma^2_w} \quad , \text{ and} \end{aligned}$$

$$H^2 = \frac{4(\sigma_{GCA}^2) + 4(\sigma_{SCA}^2)}{2(\sigma_{GCA}^2) + \sigma_{SCA}^2 + \sigma_W^2} ;$$

where σ_A^2 and σ_D^2 are the additive and dominance component of genetic variance, respectively, and h^2 and H^2 are the narrow-sense and broad-sense heritabilities. Coefficients of genetic variation (CGV) were estimated for all variables as:

$$CGV = \frac{(\sigma_A^2 + \sigma_D^2)^{1/2}}{\bar{X}} ,$$

where σ_A^2 and σ_D^2 are the genetic variances described above and \bar{X} is the trait mean.

The genetic correlations between two-month variables and ten-month variables were examined with Burdon's (1977) equation:

$$r_{g(xy)} = \frac{r_{xy}}{(h_{g(x)}^2 * h_{g(y)}^2)^{1/2}} ;$$

in which $r_{g(xy)}$ is the genetic correlation coefficient between the relative-group means of x and y and r_{xy} is the Pearson phenotypic correlation coefficient between the same group means. The narrow-sense heritabilities of group means for x and y are $h_{g(x)}^2$ and $h_{g(y)}^2$, respectively. In our experiment, full-sib families were used as genetic groups, thus the resulting genetic correlations include fractional components of both additive and non-additive genetic effects (Shaw, 1993).

RESULTS AND DISCUSSION

The trait means and genetic parameters for the seedling's vegetative growth variables are shown in Tables 1 and 2. Estimates of the additive variance (σ_A^2) were positive for all traits, but no dominance variance (σ_D^2) was detected for two-month radius, ten-month fresh weight, or growth index at either two or ten months. The narrow-sense heritabilities for the two-month variables were $h^2 = 0.23-0.47$ and the broad-sense heritabilities were $H^2 = 0.44-0.60$. These are in the moderate range for heritabilities. Conversely, at ten months the same or comparable traits had much lower heritabilities: $h^2 = 0.08-0.27$ and $H^2 = 0.13-0.27$. The trend for traits of young seedlings to have higher heritabilities than the heritabilities of the traits as the trees mature has been seen in several conifer species (Franklin, 1979). This trend in conifers was theorized is to be due to the different types of competition the perennial plant encounters during different stages of the life-cycle (Franklin, 1979; Namkoong et al., 1972). In our study, the environmental differences between growing environments may have induced this trend in the heritabilities. The first two months of growth were relatively competition free compared to the following eight months in the outdoor environment in which competition between seedlings was evident. Alternatively, the external nursery environment may have introduced greater environmental variation to heritability estimates. The latter explanation is supported somewhat by the observation that genetic coefficients of variation (Tables 1 and 2) are similar for the two environments despite average differences in heritabilities. It is likely that both competition and increased environmental heterogeneity contribute to smaller heritabilities in the nursery.

Large phenotypic and genetic correlations were detected between two-month variables and the comparable ten-month variables (Table 3). High genetic correlations indicate that the same genes are acting in both environments and at both seedling growth stages. The correlations in this study may be slightly biased upward because the same

individuals were used to calculate group means in both parts of the heritability study (Shaw, 1993).

These moderate heritabilities indicate that seedling growth traits are under genetic control and that it may be possible to modify these traits and their consequent traits with selection at this early growth stage. The age at which early selection would be most efficient needs to be assessed after juvenile-mature correlation of traits in *P. domestica* is better understood (Lambeth et al., 1983). The radius may be the most useful early seedling trait for indication of vigor. The radius has a moderate to high narrow-sense heritability at two months (0.44) and at ten months (0.20) compared to the other traits. Although the two-month growth index has similar narrow-sense heritability at two months (0.47), it is lower at ten months (0.15). The growth index may be more comprehensive for assessing general plant vigor than the radius alone because of its inclusion of both height and radius. However, the radius would be the more economically feasible characteristic to measure at both seedling stages and is less susceptible to experimental error due to the fact that it is a less subjective measurement compared to measuring the height of the multi-branched seedlings. This finding is in agreement with Muranty et al. (1998) who found that the height and girth in wild cherry were highly correlated and that girth had a higher narrow-sense heritability than height.

In the future, seedling growth traits may be shown useful as an indication of the desirability and vigor of mature trees, but more information is needed on the correlation between the characteristics at this early age compared to desired characteristics of the mature tree.

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Tables

Table 1. Means, standard error (in parenthesis), narrow-sense heritability (h^2), and broad-sense heritability (H^2) of the for *P. domestica* vegetative growth variables at two months after germination (terms defined in text).

	Two-month Radius (mm)	Two-month Height (mm)	Two-month Growth index ^z	Combined branch and trunk length (mm)
Mean	2.63 (1.00)	297.40 (108.93)	17.46 (5.28)	5.91 (0.91)
σ^2_A	0.45	2493.10	13.03	0.35
σ^2_D	0	4092.60	0	0.14
σ^2_W	0.73	8483.85	19.27	0.59
h^2	0.44	0.23	0.47	0.42
H^2	0.44	0.59	0.47	0.60
CGV	0.26	0.27	0.21	0.18

^zGrowth Index = (Radius)² * Height.

Table 2. Means, standard error (in parenthesis), narrow-sense heritability (h^2), and broad-sense heritability (H^2) of the for *P. domestica* vegetative growth variables at ten months after germination (terms defined in text).

	Ten-month Radius (mm)	Ten-month Height (cm)	Ten-month Growth index ^z	Ten-month Fresh weight (g)
Mean	116.09 (53.67)	100.87 (30.32)	76.91 (47.79)	224.18 (122.67)
σ^2_A	604.80	71.60	355.40	4131.24
σ^2_D	134.40	54.92	0	0
σ^2_W	2618.00	887.20	2152.96	13404.26
h^2	0.20	0.08	0.15	0.27
H^2	0.25	0.13	0.15	0.27
CGV	0.23	0.11	0.25	0.29

^zGrowth Index = (Radius)² * Height.

Table 3. Phenotypic (r_p) and Genetic correlations (r_g) for *P. domestica* vegetative growth variables at two months correlated to variables at ten months after germination.

Variables correlated	r_p	r_g
Radius at two months to radius at ten months	0.61	0.74
Height at two months to height at ten months	0.84	1.16
Growth index ^z at two months to growth index ^z at ten months	0.72	0.92
Combined branch and trunk length (mm) at two months to Fresh weight (g) at ten months	0.83	0.98

^zGrowth Index = (Radius)² * Height.

