# Estimation of Genetic Parameters for 12 Fruit and Vegetative Traits in the University of Florida Strawberry Breeding Population

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ABSTRACT. The University of Florida strawberry (*Fragaria ×ananassa*) breeding population has been continuously improved by recurrent selection since 1968. However, there is a lack of information on genetic parameters that may inform breeding decisions. Parameters were estimated in this population using 19 full-sib families from a 5 × 4 factorial mating design plus six additional biparental crosses and 14 control genotypes including some of the parents. During the 2010–11 season, clonal replicates of the seedling and parental genotypes were distributed within and among two field locations in west–central Florida. Twelve commercially important traits were measured including fruit chemical traits (soluble solids content and titratable acidity), other fruit and yield traits (early and total marketable yields, proportion of total cull fruit, proportion of misshapen fruit, proportion water-damaged fruit, and shape score), and vegetative traits (plant height and total runners). Heritabilities, genotype by environment interaction, and multiple correlations (phenotypic, genotypic, and genetic) were estimated using general mixed model analyses. Narrow-sense heritabilities varied from low to moderate ($h^2 = 0.13 \pm 0.07$ to $0.32 \pm 0.09$) except for shape score ($h^2 = 0.06 \pm 0.04$) and total average weight ($h^2 = 0.52 \pm 0.07$). Broad-sense heritabilities were larger ($H^2 = 0.18 \pm 0.03$ to $0.53 \pm 0.04$), and for more than half of the traits, over 50% of the total genetic variation was non-additive. Large genetic and genotypic correlations were found for some traits, most notably between soluble solids content and early marketable yield ($-0.68 \pm 0.22$). Genetic gains for this pair of traits based on a Monte Carlo simulation illustrated the tradeoff between these two traits, showing that a 27% increase in early yield could be obtained through selection but at the expense of an 8% decrease in soluble solids. However, moderate gains can be made in both traits using the appropriate index coefficients.

Florida is the primary source of strawberry fruit for the eastern United States and eastern Canada from December to late March. The state is second to California in total U.S. production with a harvested area of greater than 3600 ha during the 2010–11 season (U.S. Department of Agriculture, 2011). Production in Florida shares similarities with major production regions such as Australia, southern California, and Spain, where strawberries are grown using bare-root transplants in intensive, annualized systems for winter and spring markets.

In 1968 the University of Florida (UF) started a strawberry breeding program (Whitaker et al., 2011), although some open-pollinated seedling selection was performed before that time. Since that time, the breeding population has been continually improved for multiple plant and fruit traits through recurrent selection. Typically, ≈100 controlled crosses have been made each year among ≈30 or more parental genotypes in the main breeding population with additional crosses made for germplasm development efforts. Pedigree records have been maintained to monitor parentage and inbreeding, and full-sib crosses have almost always been avoided. To replicate commercial nursery conditions, each seedling genotype is asexually propagated through stolons (runners) in a temperate summer nursery to produce bare-root transplants for evaluation in the fruiting

field. In this way multiple runner plants per seedling genotype may be evaluated; the original seedling plant is not evaluated.

West–central Florida is characterized by periodic rainfall, high humidity, fluctuating temperatures, and occasional freezes, which inhibit pollination and fruit development, resulting in unmarketable fruit. Therefore, reducing the proportion of unmarketable fruit and thereby increasing marketable yield is an important breeding objective. The seasonality of fruit production for a strawberry cultivar is also of vital importance, in which an ideal pattern consists of large early-season yields from late November through January when the value of the crop is greatest and moderated late-season yields during February and March when overproduction can result in reduced market prices. Large average fruit size is also a breeding objective as well as favorable levels of traits that affect flavor perception such as soluble solids content (SSC) and titratable acidity (TA) (Joquand et al., 2008). In addition, the plant must be vigorous enough to establish well in the field and support high yields but no so large and dense as to restrict air movement and obscure the fruit from harvesters.

A historical trial of cultivars and advanced selections from the UF strawberry breeding program revealed gains over time for fruit size and proportion of marketable fruit (Whitaker et al., 2011). Although SSC and TA varied widely among genotypes, clear trends over time could not be observed for these traits. Until recently, there have been no published reports of genetic parameters such as heritabilities and genetic correlations for the

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UF strawberry breeding population, which would be desirable for shaping breeding and selection strategies (Hasing et al., 2011). They provide an understanding of the effects of trait selection in the long term and the behavior of correlated traits that, if adverse, may hinder breeding progress if they are ignored during selection.

Previous studies have reported genetic parameters for plant and fruit traits of strawberries in both annual and perennial production systems (reviewed by Galleta and Maas, 1990; Hancock et al., 2008). Information on genetic parameters for annual production systems have mainly been generated using the University of California–Davis breeding population. Narrow-sense heritabilities for plant growth traits such as plant diameter have been low to moderate with little contribution of non-additive variance (Fort and Shaw, 2000; Shaw, 1993). Substantial amounts of additive variance for yield and fruit size have been demonstrated, although the relative proportions of additive and dominance variance have varied widely across testing environments and propagule types (Fort and Shaw, 2000; Pringle and Shaw, 1998; Shaw, 1989; Shaw et al., 1989; Shaw and Larson, 2005). Greater dominance variance was typically found for SSC and TA (Shaw et al., 1987). Gains from selection for SSC were predicted to be poor based on clonal trials of selected individuals, mainly as a result of large interactions with cultural environments and harvest dates (Shaw, 1988, 1990).

Although these previous studies provide important benchmarks, they may not be reflective of the germplasm, population history, and testing environments of the UF strawberry breeding program. In this study, we explore the genetic basis of several important fruit and vegetative traits in the UF strawberry breeding population by conducting clonal tests of seedling, parental, and control genotypes across two environments and performing genetic analyses that incorporate pedigree records spanning 15 generations. Specifically we aim to: 1) obtain estimates of narrow-sense heritability, broad-sense heritability, and genotype by environment interactions; 2) estimate phenotypic, genotypic (additive plus non-additive genetic effects), and genetic (additive) correlations among the traits of interest; and 3) predict genetic gains from multivariate selection.

## Materials and Methods

**Mating and field designs.** Twenty-five biparental crosses were generated for testing by controlled pollination among 17 parents. Nineteen biparental crosses were made among nine parents in a 5 × 4 factorial mating design (one cross missing). These parents were chosen to represent a broad range of phenotypic diversity present in the breeding program. Six additional biparental crosses were made among 10 different parents. These crosses were a random sample of the crosses already generated in the breeding program for evaluation during the 2010–11 season. Two parental genotypes were shared across the factorial crosses and the additional biparental crosses. All parents shared pedigree linkages and constituted a representative selection of named cultivars and advanced selections from the UF strawberry breeding program. Seventeen parents was considered a sufficient sample size to represent the main UF strawberry breeding population, which is maintained through controlled crosses among 25 to 30 parents each year and contains several connecting relatives from previous generations. Twenty seedlings were chosen at random from each cross for testing. In addition, 14 control genotypes were included, which arose from 23 different parents. These genotypes were either parents or other advanced selections.

In 2010 all seedlings were germinated and transported to the breeding program's summer nursery site in Monte Vista, CO (lat. 37°40′46.10″ N, long.106°8′10.83″ W) where they were clonally propagated by runners. Four bare-root runner plants were generated from each seedling and for each of the 13 additional parental and advanced selection genotypes. Before planting, transplants were individually weighed (grams) to determine initial runner plant weight. Two runner plants were established at the Gulf Coast Research and Education Center (GCREC) in Balm, FL (lat. 27°45′37.98″ N, long. 82°13′32.49″ W) on 11 Oct. 2010, and two runner plants were established at the test plots of the Florida Strawberry Growers Association in Dover, FL (lat. 28°0′55.55″ N, long. 82°14′5.24″ W) on 14 Oct. 2010. At each site the runner plants were arranged in a randomized block design (single-plant plots resulting in four total replications across sites) with two raised beds per replication in Balm and three beds per replication in Dover.

Each site was prepared and maintained according to standard commercial practices, which are more fully described in Mackenzie et al. (2011). Briefly, beds were 91.5 m long, 71 cm wide, 15 cm high at the edges, and 18 cm high in the center and were fumigated with a mixture of telone and chloropicrin ≈1 month before transplanting. There were two offset rows of plants per bed. Plant spacing was 38 cm within rows and 28 cm between rows. After transplanting the runner plants were overhead-irrigated for 10 d during daylight hours to facilitate establishment. Once established, the plants were irrigated and fertilized exclusively through the drip tape.

**Data collection.** Data for all traits were gathered on an individual plant basis. Each runner plant was weighed to determine its initial weight in grams before establishment. Fruit harvests were made at weekly intervals beginning with the appearance of the first ripe fruit in late November and continuing until the end of January. As a result of restrictions in available labor for harvesting as yields increased, late-season fruit harvests were recorded every other week during February and March, similar to the partial records method of Shaw (1989) where yield was recorded on alternate weeks.

Two fruit chemical traits, SSC and TA, were assessed. The SSC trait was measured in the field four times between 11 Jan. and 30 Mar. 2011 and is expressed as the mean over time of all individual measurements. One or two ripe fruit were squeezed by hand until the expressed juice covered the prism of a handheld digital refractometer (PAL-1; Atago Co., Tokyo, Japan) that was calibrated with deionized (DI) water. On 8 to 9 Mar. 2011 juice samples were collected for measurement of TA. One or two fruit (depending on availability) per plant were squeezed by hand and the juice collected with a funnel into a 6-mL screw-capped plastic vial. The vials were placed on ice and transported to the GCREC laboratory where they were frozen at –20 °C. At the conclusion of the season, the vials were thawed and 1 to 2 mL of juice was diluted with 50 mL DI water and titrated with 0.1 N NaOH to a pH 8.1 end point using a 719 S titraino and 738 stirrer (Metrohm USA, Westbury, NY). The ratio SSC/TA was calculated and included in the analysis as a separate trait because it is known that this ratio influences flavor perception in UF strawberry cultivars (Joquand et al., 2008).

Seven additional yield and fruit traits were assessed. At each harvest, all ripe fruit were removed and counted. Marketable

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fruit were weighed (grams) to determine total marketable yield (TMY). Early marketable yield (EMY) was calculated as the marketable weight before the first harvest in February. The TMY was divided by the number of marketable fruit to estimate average fruit weight (AWT). The total number of unmarketable (cull) fruit was counted and expressed as a proportion of the total number of fruit (TC). Cull fruit were further rated into overlapping subcategories including total misshapen fruit (TM) and total water-damaged fruit (TWD), which were also expressed as a proportion of the total number of fruit. Marketable fruit were rated for shape during three different harvests between 11 Jan. and 23 Feb. Each fruit was subjectively categorized on a 1 to 3 pictorial scale, where a rating of "1" represented fruit with irregular shape and surface and a rating of "3" represented fruit with regular conical shape and minimal surface irregularities. A weighted mean shape score (SHP) was calculated by multiplying the number of fruit in each scale category by their scores and dividing by the total number of fruit in all categories.

Two vegetative traits, total runners (TRs) and plant height (PHT), were also assessed. All runners produced between 30 Nov. 2010 and 4 Jan. 2011 were removed and counted. Plant height (centimeters) was measured on 25 to 27 Jan. 2011 using a straight ruler.

STATISTICAL AND GENETIC ANALYSES. A covariance analysis across locations was carried out using ASReml software (Gilmour et al., 2009) to test the effect of including initial runner plant weight in grams as a fixed covariate in the model. Significance of the covariate was assessed by the incremental Wald statistic.

Univariate and bivariate analyses for all traits were conducted using ASReml software (Gilmour et al., 2009). Univariate analyses were performed to generate variance components for the bivariate analysis and the type B genetic correlations between locations (Yamada, 1962). These correlations allow the estimation of genotype by environment interaction at both the additive and genotypic (additive plus non-additive) levels. Type B correlation values range from 0 to 1, and values close to 1 indicate a low genotype by environment interaction. The tested families had some relatedness among them causing some bias of the genetic estimates, but the bias was ameliorated by incorporating a pedigree structure to the model. The 14 control genotypes were included in the analyses to calculate variance components, and pedigree information was incorporated for each of them as well. The univariate analyses were undertaken following the general mixed model:

$$y = Xb + Z_1a + Z_2c + Z_3k + Z_4l + e \qquad (1)$$

where $y$ is the vector of observations; $b$ is the vector including the population mean, sites, replications, and the covariate fixed effects; $a$ is the vector of random additive effects; $a \sim NID\left(0, A\sigma_a^2\right)$ $c$ is the vector of non-additive genetic effects, including dominance plus epistasis and $c \sim NID\left(0, C\sigma_c^2\right)$; $k$ is the vector of random interactions between location and additive effects; and $k \sim NID\left(0, I_s\sigma_{as}^2\right)$ $l$ is the vector of random interactions between location and non-additive effects, $l \sim NID\left(0, I_s\sigma_{cs}^2\right)$. Heterogeneity of the residual effects across locations was modeled as $e \sim NID(0, R)$, $wit$ $IR = \oplus I_{nj}\sigma_{ej}^2$ where $j$ is the location and $\oplus$ defines the direct sum operation. $A$ is the matrix of additive relationships among genotypes, $C$ is the matrix of non-additive effects, and $I_s$ is an identity matrix

with $s$ equal to the number of sites. $\sigma_a^2$, $\sigma_c^2$, $\sigma_{as}^2$, $\sigma_{cs}^2$ and $\sigma_{ej}^2$ are the additive genetic variance, non-additive genetic variance, additive by site interaction variance, non-additive by site interaction variance, and variances of random residual effects. $X$, $Z_1$, $Z_2$, $Z_3$, and $Z_4$ are known incidence matrices relating the observations in $y$ to effects in $b$, $a$, $c$, $k$, and $l$. The bed effects were not included in the model because beds within replication effects had been proven not significant in a previous study at the same locations designed to account for spatial variability along the beds (unpublished data).

Narrow sense heritability ($I^2$) and broad sense heritability ($H^2$) for each variable were estimated as follows:

$$I^2 = \frac{\sigma_a^2}{\sigma_a^2 + \sigma_c^2 + \sigma_{as}^2 + \sigma_{cs}^2 + \frac{\sum_{j=1}^{2}\sigma_{ej}^2}{2}} \qquad (2)$$

and

$$H^2 = \frac{\sigma_a^2 + \sigma_c^2}{\sigma_a^2 + \sigma_c^2 + \sigma_{as}^2 + \sigma_{cs}^2 + \frac{\sum_{j=1}^{2}\sigma_{ej}^2}{2}} \qquad (3)$$

with $\sigma_a^2$, $\sigma_c^2$, $\sigma_{as}^2$, $\sigma_{cs}^2$ and $\sigma_{ej}^2$ as previously defined. Type B genetic correlations were estimated using the formula (Yamada, 1962):

$$r_{B_a} = \frac{\sigma_a^2}{\sigma_a^2 + \sigma_{as}^2} \quad \text{and} \quad r_{B_g} = \frac{\sigma_a^2 + \sigma_c^2}{\sigma_a^2 + \sigma_c^2 + \sigma_{as}^2 + \sigma_{cs}^2} \qquad (4)$$

where $r_{B_a}$ and $r_{B_g}$ are the additive type B genetic correlation and genotypic type B correlation.

A reduced model without the additive by site and non-additive by site random interaction effects was used for the bivariate analyses as a result of lack of convergence of the parameters when the full model was used. The bivariate analyses between all traits were based on the following mixed model equation:

$$y = Xb + Z_1a + Z_2c + e \qquad (5)$$

where $y$ is a stacked vector of observations for traits 1 ($t_1$) and 2 ($t_2$); $b$ is the stacked vector of means, sites, replications within site fixed effects, and the covariate fixed effect; $a$ is the stacked vector of random additive effects and $a \sim MVN(0, G \otimes A)$, $G = \begin{bmatrix} \sigma_{a_{t1}}^2 & \sigma_{a_{t1,t2}} \\ \sigma_{a_{t2,t1}} & \sigma_{a_{t2}}^2 \end{bmatrix}$ and $A$ is the numerator relationship matrix among genotypes; $c$ is the vector of non-additive random effects and $c \sim MVN(0, C \otimes I_c)$, where $C = \begin{bmatrix} \sigma_{c_{t1}}^2 & \sigma_{c_{t1,t2}} \\ \sigma_{c_{t2,t1}} & \sigma_{c_{t2}}^2 \end{bmatrix}$ and $I_c$ is the identity matrix with order equal to the number of clones within families; $e$ is the vector of random residual effects $e \sim MVN(0, R)$, where $R = \begin{bmatrix} \sigma_{e_{t1}}^2 & 0 \\ 0 & \sigma_{e_{t2}}^2 \end{bmatrix}$. The components $\sigma_{a_{t1}}^2$, $\sigma_{a_{t2}}^2$, $\sigma_{a_{t1,t2}}$ are the additive variance for trait 1, trait 2, and the additive covariance between traits 1 and 2; and $\sigma_{e_{t1}}^2$, $\sigma_{e_{t2}}^2$ are the residual errors for trait 1 and 2, respectively.

The bivariate analysis supplied breeding values for all tested individuals and their relatives back 15 generations. Estimates of additive, genotypic (additive plus non-additive), and phenotypic correlations for pairs of traits were obtained according to the following equation:

$$r_{t_1 t_2} = \frac{\sigma_{t_1 t_2}}{\sqrt{\sigma_{t_1}^2 * \sigma_{t_2}^2}} \qquad (6)$$

where $r_{t_1 t_2}$ is the genetic, genotypic, or phenotypic correlation between trait 1 and trait 2; $\sigma_{t_1 t_2}$ is the genetic, genotypic, or phenotypic covariance between two traits; and $\sigma_{t_1}^2$, $\sigma_{t_2}^2$ are the genetic, genotypic, or phenotypic variances of trait 1 and trait 2.

ESTIMATION OF GENETIC GAINS. As a result of a strong and negative genetic correlation between EMY and SSC, expected genetic gains for these two traits were simulated by the generation of an index using a Monte Carlo iteration process (Cotterill and Dean, 1990). The index was calculated by assigning sequential weights ($w_i$) to the breeding value (BV) of each trait and individual. A set of 20 varying weights ranging from 0 and 1, whose sum add to one, were used (i.e., index = $0.7 \times BV\_t_1 + 0.3 \times BV\_t_2$). At each combination of weights, the top 10% of individuals in the population were ranked for each trait and their average breeding value was expressed as expected gain over the population mean across the two locations.

## Results

Summary statistics for all tested traits in Balm and Dover are reported in Table 1. Although EMY was slightly higher in Balm than in Dover, TMY was the same at both sites by the end of the season. Results from the across site covariance analyses indicated that initial runner plant weight was significant ($P < 0.05$) for PHT, EMY, and TMY (data not shown); therefore, it was included as a factor in the univariate and bivariate statistical models for only those traits.

Broad sense heritability for most traits indicated a moderate degree of genotypic control ($H^2 = 0.30$ to 41) except for SHP, which had a low broad sense heritability ($H^2 = 0.18 \pm 0.03$), and AWT, which possessed strong genotypic control ($H^2 = 0.53 \pm 0.04$) (Table 2). Narrow-sense heritability estimates were mainly low ($h^2 = 0.13$–0.32) and were very low for SHP ($h^2 = 0.06 \pm 0.04$), indicating that for half of the traits, more than 50% of the total genetic variation was the result of non-additive

genetic effects. Non-additive effects were present in all traits except AWT in which all genetic variation was the result of additive genetic variance. The genotype by environment interactions ($G \times E$) for the additive effects, determined by the type B genetic correlations, were very low (type B correlations greater than 0.70) for all traits. Similarly, $G \times E$ for genotypic (additive plus non-additive) effects was also very low, demonstrating the repeatability of clonal performance across the two sites (Table 2).

A total of 66 pair sets of correlations (phenotypic, genotypic, and genetic) was estimated for the 12 traits under consideration (Table 3). Only 17 sets of correlations had at least one estimate with acceptable SEs (italics) and were moderate to high (bold). An acceptable SE was considered to be less than half of the variance estimate as suggested by other authors (Isik et al., 2003). The remaining correlations had SEs higher than half the estimate making them of little practical use. Notable additive genetic correlations include negative associations of SSC with EMY ($-0.68 \pm 0.22$) and with TMY ($-0.76 \pm 0.15$), indicating that selection over time for higher SSC could result in reduced breeding progress for yield traits. The TM and SHP traits also had a strong genetic correlation ($-0.58 \pm 0.27$) indicating that selection for a decreased proportion of misshapen fruit would also result in more uniform and regular shape of the marketable portion of the fruit. Notable additive correlations were also found among fruit and vegetative traits such as between TMY and PHT ($0.58 \pm 0.20$) and between TMY and TR ($0.50 \pm 0.25$), showing that there is a positive genetic relationship between vegetative vigor and yield. There were several additive and genotypic correlations close to zero indicating independence of the genetic control of the traits (e.g., EMY and TM); however, their SEs usually ranged between 0.10 and 0.36 (Table 3).

Genetic gains for SSC and EMY based on breeding values for the top 10% of individuals showed that high gains in early marketable yield might be obtained but at the expense of SSC as a result of the unfavorable correlation between these traits (Fig. 1). With an index coefficient of 0.0 for SSC and 1.0 for EMY, a gain of 27% in EMY would be offset by a decrease in SSC of ≈8%. With index coefficients of 0.7 for SSC and 0.3 for EMY, gains would be modest but equal for the two traits. A maximum gain of 12% for SSC would cause a loss of 8% in EMY.

Breeding values for the 17 parents and their summary statistics as well as summary statistics for the breeding values of the progeny are reported in Table 4. The negative genetic correlations between SSC and EMY and SSC and TMY are apparent when comparing breeding values of parents across columns. The range of breeding values for the progeny exceed the range of breeding values for the parents for all traits except TWD and EMY. The narrow range of breeding values for TWD reflect the low narrow-sense heritability of this trait. For EMY, the mean and range of breeding values are shifted toward larger values in the progeny compared with the parents, indicating potential for further gains.

## Discussion

The descriptive statistics in Table 1 illustrate the broad phenotypic variation in the population for all fruit and vegetative traits, particularly for the fruit traits related to yield and culls. Proportions of cull fruit may be large in some Florida seasons as a result of fluctuating environmental conditions. In 2010–11 an abnormally high number of freezes contributed to

Table 1. Descriptive statistics for 12 fruit and vegetative traits in the University of Florida strawberry breeding population from 1919 observations across two locations (Balm, FL and Dover, FL) during the 2010–11 season.

| Trait | Balm<br>2Mean (SD) | Dover<br>Mean (SD) |
|---|---|---|
| Fruit chemical traits | | |
| Titratable acidity (TA) (%) | 0.54 (0.16) | 0.45 (0.13) |
| Soluble solids content (SSC) (%) | 7.14 (1.35) | 6.47 (1.40) |
| SSC/TA | 10.8 (3.04) | 11.6 (3.22) |
| Yield and fruit traits | | |
| Average fruit weight (g) | 20.2 (4.3) | 21.8 (5.1) |
| Early marketable yield (g) | 86.1 (59.3) | 75.4 (53.1) |
| Total marketable yield (g) | 312.2 (155.5) | 312.3 (152.5) |
| Total season cull fruit (%) | 42 (17) | 34 (18) |
| Total season misshapen fruit (%) | 9 (9) | 15 (13) |
| Total season water-damaged fruit (%) | 17 (14) | 11 (13) |
| Shape score (weighted mean score) | 1.92 (0.4) | 1.96 (0.6) |
| Vegetative traits | | |
| Plant height (cm) | 16.0 (3.3) | 15.1 (3.8) |
| Total number of runners | 5.3 (3.9) | 3.5 (2.1) |

Table 2. Broad-sense heritability ($H^2$), narrow-sense heritability ($h^2$), proportion of non-additive variance ($d^2 + i^2$), and the type B genetic correlation among locations (Balm, FL, and Dover, FL) for additive and genotypic (additive plus non-additive) effects of 12 fruit and vegetative traits in the University of Florida strawberry breeding population during the 2010–11 season.[z]

| | $H^2$ (SE) | $h^2$ (SE) | $d^2 + i^2$ (SE) | $r_{B\_additive}$ (SE) | $r_{B\_genotypic}$ (SE) |
|---|---|---|---|---|---|
| Fruit chemical traits | | | | | |
| TA | 0.36 (0.04) | 0.13 (0.07) | 0.23 (0.05) | 0.85 (0.12) | 0.94 (0.04) |
| SSC | 0.30 (0.04) | 0.21 (0.08) | 0.09 (0.05) | 0.96 (0.06) | 0.97 (0.04) |
| SSC/TA | 0.37 (0.04) | 0.22 (0.07) | 0.14 (0.05) | 0.87 (0.10) | 0.84 (0.07) |
| Yield and fruit traits | | | | | |
| AWT | 0.53 (0.04) | 0.52 (0.07) | 0.00 | 0.96 (0.03) | 0.96 (0.03) |
| EMY | 0.39 (0.04) | 0.18 (0.07) | 0.22 (0.05) | 0.88 (0.10) | 0.92 (0.06) |
| TMY | 0.36 (0.05) | 0.23 (0.10) | 0.13 (0.06) | 0.80 (0.14) | 0.81 (0.07) |
| TC | 0.30 (0.04) | 0.16 (0.08) | 0.15 (0.05) | 0.70 (0.17) | 0.82 (0.09) |
| TM | 0.36 (0.05) | 0.23 (0.11) | 0.14 (0.07) | 0.92 (0.07) | 0.95 (0.04) |
| TWD | 0.40 (0.03) | 0.13 (0.07) | 0.27 (0.05) | 0.90 (0.10) | 0.97 (0.03) |
| SHP | 0.18 (0.03) | 0.06 (0.04) | 0.12 (0.03) | 0.84 (0.23) | 0.94 (0.08) |
| Vegetative traits | | | | | |
| PHT | 0.41 (0.04) | 0.32 (0.09) | 0.09 (0.06) | 0.97 (0.04) | 0.97 (0.06) |
| TR | 0.37 (0.03) | 0.18 (0.07) | 0.20 (0.04) | 0.84 (0.10) | 0.92 (0.05) |

[z]Fruit chemical traits include titratable acidity (TA), soluble solids content (SSC), and the SSC/TA ratio. Yield and fruit traits include average fruit weight (AWT), early marketable yield (EMY), total marketable yield (TMY), total cull fruit (TC), total misshapen fruit (TM), total water-damaged fruit (TWD), and fruit shape score (SHP). Vegetative traits are plant height (PHT) and total runners (TR).

large average cull rates of 42% and 34% at Balm and Dover, respectively. Because only partial records were kept of yield during February and March, the yield numbers reported in Table 1 are not representative of actual total production. It has been previously demonstrated that a partial records approach in which yields are recorded every other week can save labor expense while maintaining selection efficiency (Shaw, 1989).

All type B additive and genotypic correlations were 0.70 or greater (with an average of 0.87 and 0.92 for additive and genotypic, respectively), indicating that G × E was not important across the two testing locations during the 2010–11 season. Therefore, it might be concluded that testing could be carried out at a single site. Indeed, the west–central Florida growing region is relatively geographically compact and homogeneous in terms of soil types and weather conditions. However, it would be advisable to examine environmental interactions among the sites in additional years before making the decision to eliminate one of the testing locations and to evaluate G × Y interactions. Different weather conditions or cultural management between the sites in future years may result in more substantial genetic by location interactions.

Non-additive effects were present in most traits, and in half of the cases, they were equal to or larger than the additive variance of the traits (Table 2). Therefore, the use of breeding values for parent selection would be expected to improve genetic gain over time compared with the use of clonal values alone. Dominance effects have been previously reported for SSC and TA (Shaw, 1990; Shaw et al., 1987), early yield traits and total yield traits (Shaw, 1989; Shaw and Larson, 2005), and average fruit weight (Shaw et al., 1989). On the other hand, AWT displayed a high narrow-sense heritability (0.52 ± 0.07) and a lack of non-additive variance in the present study, indicating the strong potential to improve this trait by selecting the best parents. This estimate is much larger than those reported previously in California [$h^2 = 0.14$ to 0.28 (Shaw, 1989)].

Flavor is a sensory trait influenced by the fruit chemical traits of SSC, TA, and the ratio between these two variables (SSC/TA). As a strawberry fruit matures, sugars that contribute

to sweetness perception increase, organic acids and phenolic compounds decrease, and aromatic volatiles increase to produce the characteristic flavor of the ripe fruit (Nunez, 2008). A minimum of 7% SSC and a maximum of 0.8% for TA have been considered benchmarks for good eating quality (Mitcham et al., 2011). In the present study, mean values for SSC (6.47% to 7.14%) and TA (0.45% to 0.54%) were within suitable ranges but were slightly lower than those reported in other breeding populations and environments (Shaw et al., 1987). It should be noted that TA was measured at only one time point and will likely fluctuate as a result of fruiting cycles and seasonal variation. Therefore, genetic parameters for TA may not be representative for all periods during the season. The SSC trait was measured at up to four different time points for a given genotype, which is similar to previous studies in California where SSC was measured either three or four times within a single season (Shaw, 1990; Shaw et al., 1987).

Estimates of narrow-sense heritabilities for SSC and SSC/TA indicate that further gains can be made in these traits by parental selection (Table 2). In addition, these traits had moderate broad-sense heritability ($H^2 = 0.30 \pm 0.04$ to $0.37 \pm 0.04$), suggesting that clonal selection will allow the capture of non-additive variance in the deployment population. Broad-sense heritability was moderate for TA ($H^2 = 0.36 \pm 0.04$), which exhibited non-additive variance almost two times larger than the additive variance present for the trait ($h^2 = 0.13 \pm 0.07$). This is consistent with previous estimates of sizable non-additive genetic effects for these traits (Shaw et al., 1987).

The phenotypic, genetic, and genotypic correlations between SSC and TA were moderate to high indicating that directional breeding will increase both traits simultaneously (Table 3). Negative and strong additive genetic correlations were found between SSC and both EMY (–0.68 ± 0.22) and TMY (–0.76 ± 0.15) showing that these traits are controlled by genes acting in opposite directions. It is possible that after repeated cycles of simultaneous selection for these two traits, the genetic correlation has become negative because most of the covariance between them is the result of pleiotropic loci

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Table 3. Phenotypic (below diagonal), genotypic (above diagonal, lower), and genetic (above diagonal, upper) correlations and their SEs among 12 fruit and vegetative traits in the University of Florida strawberry breeding program assessed at two locations (Balm, FL, and Dover, FL) during the 2010–11 season.[z]

**Correlation (SE)**

| | TA | SSC | SSC/TA | AWT | EMY | TMY | TC | TM | TWD | SHP | PHT | TR |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| TA | | **0.58 (0.20)** / **0.52 (0.10)** | **−0.56 (0.20)** / **−0.73 (0.05)** | −0.05 (0.28) / −0.08 (0.11) | −0.06 (0.38) / −0.29 (0.08) | −0.35 (0.30) / −0.41 (0.09) | −0.04 (0.35) / 0.01 (0.11) | 0.36 (0.32) / 0.23 (0.11) | −0.04 (0.36) / 0.02 (0.09) | −0.57 (0.29) / −0.18 (0.11) | −0.17 (0.30) / −0.01 (0.11) | 0.02 (0.33) / 0.01 (0.10) |
| SSC | **0.47 (0.04)** | | −0.10 (0.14) / −0.04 (0.10) | −0.38 (0.19) / −0.25 (0.11) | **−0.68 (0.22)** / −0.28 (0.09) | **−0.76 (0.15)** / **−0.47 (0.09)** | 0.33 (0.28) / 0.13 (0.12) | −0.03 (0.32) / −0.13 (0.12) | −0.15 (0.31) / 0.09 (0.11) | −0.23 (0.33) / −0.18 (0.12) | −0.01 (0.29) / −0.06 (0.13) | −0.39 (0.27) / −0.14 (0.10) |
| SSC/TA | **−0.67 (0.02)** | 0.16 (0.04) | | −0.15 (0.21) / −0.10 (0.11) | −0.49 (0.26) / 0.04 (0.09) | −0.20 (0.28) / 0.09 (0.11) | 0.34 (0.26) / 0.06 (0.11) | −0.27 (0.27) / −0.23 (0.10) | 0.06 (0.29) / −0.06 (0.09) | 0.41 (0.27) / 0.13 (0.11) | −0.11 (0.25) / −0.15 (0.11) | −0.30 (0.27) / −0.14 (0.09) |
| AWT | −0.03 (0.05) | −0.10 (0.05) | −0.07 (0.05) | | −0.37 (0.26) / −0.10 (0.09) | 0.29 (0.22) / 0.20 (0.11) | **−0.44 (0.21)** / −0.20 (0.10) | 0.18 (0.26) / 0.11 (0.12) | **0.51 (0.22)** / 0.36 (0.08) | −0.06 (0.32) / 0.05 (0.12) | **0.44 (0.16)** / 0.31 (0.09) | **0.47 (0.21)** / 0.15 (0.09) |
| EMY | *−0.13 (0.03)* | *−0.10 (0.04)* | 0.04 (0.04) | −0.05 (0.04) | | **0.54 (0.21)** / **0.69 (0.06)** | −0.10 (0.38) / −0.26 (0.09) | −0.06 (0.39) / −0.11 (0.09) | −0.27 (0.35) / −0.22 (0.08) | 0.14 (0.41) / 0.26 (0.10) | 0.25 (0.30) / 0.15 (0.09) | 0.08 (0.35) / −0.04 (0.08) |
| TMY | *−0.20 (0.04)* | *−0.21 (0.04)* | 0.04 (0.04) | 0.21 (0.05) | 0.57 (0.03) | | **−0.72 (0.17)** / **−0.62 (0.07)** | **−0.59 (0.23)** / −0.43 (0.10) | 0.02 (0.34) / −0.21 (0.10) | **0.55 (0.28)** / **0.44 (0.10)** | **0.58 (0.20)** / **0.50 (0.09)** | **0.50 (0.25)** / 0.17 (0.09) |
| TC | −0.04 (0.04) | 0.08 (0.04) | 0.07 (0.04) | −0.08 (0.05) | −0.27 (0.03) | **−0.58 (0.03)** | | 0.41 (0.28) / 0.43 (0.10) | −0.18 (0.28) / 0.38 (0.08) | 0.39 (0.33) / −0.25 (0.13) | −0.46 (0.24) / −0.32 (0.10) | **−0.53 (0.25)** / −0.24 (0.09) |
| TM | 0.06 (0.04) | −0.08 (0.04) | −0.10 (0.04) | 0.06 (0.05) | −0.16 (0.04) | −0.33 (0.04) | 0.44 (0.03) | | 0.23 (0.35) / 0.00 (0.10) | **−0.58 (0.27)** / **−0.60 (0.09)** | −0.07 (0.29) / −0.05 (0.12) | −0.00 (0.33) / −0.03 (0.10) |
| TWD | −0.02 (0.04) | 0.03 (0.04) | −0.01 (0.04) | 0.23 (0.04) | −0.16 (0.03) | −0.24 (0.04) | 0.44 (0.03) | −0.03 (0.04) | | 0.27 (0.36) / −0.00 (0.11) | −0.11 (0.30) / −0.08 (0.10) | 0.38 (0.29) / 0.01 (0.10) |
| SHP | −0.06 (0.03) | −0.03 (0.03) | 0.06 (0.03) | 0.02 (0.04) | 0.10 (0.03) | 0.12 (0.04) | −0.09 (0.03) | −0.21 (0.03) | −0.02 (0.03) | | 0.41 (0.30) / 0.13 (0.11) | 0.12 (0.35) / −0.05 (0.10) |
| PHT | −0.02 (0.04) | −0.10 (0.05) | −0.06 (0.04) | *0.20 (0.05)* | 0.07 (0.04) | *0.37 (0.04)* | −0.19 (0.04) | −0.01 (0.05) | −0.05 (0.04) | 0.02 (0.03) | | **0.66 (0.18)** / 0.37 (0.08) |
| TR | 0.02 (0.04) | −0.06 (0.03) | −0.05 (0.04) | *0.09 (0.04)* | −0.07 (0.03) | 0.08 (0.04) | *−0.09 (0.03)* | 0.03 (0.04) | 0.00 (0.04) | −0.05 (0.03) | 0.26 (0.03) | |

[z]Fruit chemical traits include titratable acidity (TA), soluble solids content (SSC), and the SSC/TA ratio. Yield and fruit traits include average fruit weight (AWT), early marketable yield (EMY), total marketable yield (TMY), total cull fruit (TC), total misshapen fruit (TM), total water-damaged fruit (TWD), and fruit shape score (SHP). Vegetative traits are plant height (PHT) and total runners (TR). Correlations for which SEs (in parentheses) are less than half of the estimate are in italicized font, and correlations considered to have moderate to high magnitude are in bold font.

affecting one character favorably and the other adversely (Falconer, 1989). The phenotypic correlation between SSC and EMY or TMY was slightly low and negative (Table 3). Studies on Italian cultivars have shown a negative phenotypic correlation between yield and SSC with the most productive clones having low sugar content (Faedi et al., 2002). During the

Florida growing season, temperatures are often high, particularly at night, compared with coastal California environments. It has been shown that high temperatures in Florida can cause reduced SSC (Mackenzie et al., 2011). Under such conditions when available carbohydrates are presumably limited, there may be a tradeoff between the total fruit load on the plant and the concentration of soluble solids in the fruit.

The Monte Carlo simulation to estimate genetic gains for SSC and EMY has the advantage of allowing the breeder to choose the index values for the two traits that provides the optimum level of gains for each trait. Selection index weights for SSC between 0.6 and 0.75 provide genetic gains from 1% to 11% for SSC and from 20% to 0.5% for EMY (Fig. 1). Although the negative genetic correlation between the traits is strong, the selection of weights within the range previously described allowed the choice of several genotypes with positive breeding values for both traits (Table 4). However, as a result of the low precision on the estimation of this genetic correlation, these results should be considered with care. An economic analysis would be desirable to guide the choice of appropriate selection indices. It is generally assumed by Florida strawberry growers that greater early yields would result in increased profitability. An economic analysis conducted in Queensland, Australia, a region with similar climate to Florida and using some of the same cultivars, showed that a 10% redistribution of yield from the end to the beginning of the season should result in a gross margin increase of 23% (Herrington et al., 2012).
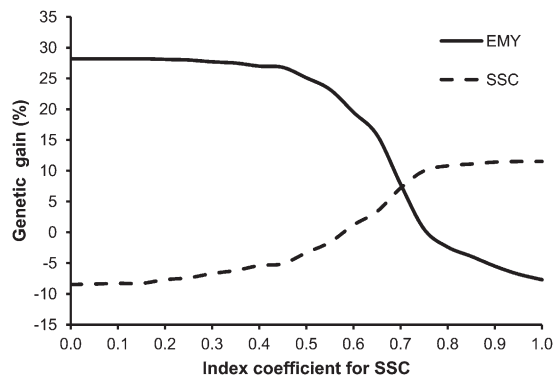


Fig. 1. Genetic gains for early marketable yield (EMY) and soluble solids content (SSC) from a Monte Carlo simulation in which the top 10% of strawberry genotypes are selected from the University of Florida strawberry breeding population. The index coefficients for EMY and SSC sum to 1.0; thus, an index coefficient of 1.0 for SSC means that the index coefficient for EMY is 0.0 and vice versa.

Table 4. Breeding values of 17 parents for 12 fruit and vegetative traits in the University of Florida strawberry breeding program assessed at two locations (Balm, FL, and Dover, FL) during the 2010–2011 season, expressed as deviations from the population means which are close to zero.[z]

| | Breeding value | | | | | | | | | | | |
| | Fruit chemical traits | | | Yield and fruit traits | | | | | | | Vegetative traits | |
| Parent | TA (%) | SSC (%) | SSC/TA | AWT (g) | EMY (g) | TMY (g) | TC (%) | TM (%) | TWD (%) | SHP (score) | PHT (cm) | TR (count) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Radiance | –0.03 | –0.88 | –1.46 | 0.47 | 24.12 | 119.10 | –4.57 | –3.75 | –1.52 | 0.07 | 2.44 | 0.40 |
| FL 06-45 | 0.03 | –1.05 | –1.91 | 0.41 | 32.70 | 99.87 | –7.08 | –5.70 | 2.19 | –0.02 | –0.35 | 0.44 |
| FL 05-107 | –0.05 | –0.80 | –0.37 | –0.05 | 4.72 | 64.32 | –5.36 | –4.91 | –2.84 | 0.09 | 2.14 | 0.70 |
| FL 01-92 | –0.03 | –0.68 | 0.52 | –2.30 | –10.05 | 64.19 | 2.47 | –1.88 | –0.48 | 0.06 | 1.21 | 1.30 |
| FL 06-58 | –0.02 | –0.52 | –1.22 | –3.17 | 19.60 | 31.11 | 2.72 | 0.18 | 2.67 | 0.00 | –0.82 | 0.90 |
| FL 05-105 | 0.02 | –0.21 | –1.24 | –3.17 | 9.89 | 26.42 | 3.21 | –4.34 | –0.88 | 0.04 | –0.54 | –1.52 |
| FL 06-38 | 0.09 | 0.10 | –1.93 | 3.46 | 5.75 | 16.85 | –0.31 | 2.14 | 3.78 | 0.04 | 1.50 | 0.82 |
| FL 05-73 | 0.01 | –0.01 | –0.83 | –1.26 | –28.03 | 16.08 | 0.31 | –4.08 | 0.96 | 0.06 | 1.98 | 0.37 |
| FL 06-89 | –0.03 | 0.13 | 0.36 | 3.69 | 9.28 | 14.21 | –1.88 | 4.32 | –2.01 | –0.05 | 2.12 | 0.18 |
| FL 06-46 | 0.05 | –0.92 | –3.09 | –1.65 | 19.77 | 3.81 | –1.45 | 5.76 | –2.84 | –0.11 | 0.85 | 1.43 |
| FL 07-122 | 0.01 | 0.89 | 0.90 | –5.80 | –2.82 | 1.22 | –6.48 | –4.21 | –10.01 | –0.09 | 0.56 | –0.22 |
| FL 02-16 | 0.01 | 0.37 | 1.09 | –4.98 | 13.78 | –29.01 | 9.62 | 0.13 | 2.12 | 0.08 | 0.46 | –0.70 |
| FL 05-150 | 0.01 | 0.42 | –0.02 | –3.46 | –8.78 | –35.61 | 2.65 | –4.52 | 0.89 | 0.02 | –1.16 | –0.69 |
| FL 05-85 | –0.06 | 0.10 | 2.16 | –4.44 | 2.26 | –43.44 | 7.71 | –0.42 | –2.99 | 0.10 | –1.99 | –1.51 |
| FL 02-58 | –0.06 | 0.27 | 3.05 | 3.36 | –44.48 | –44.60 | 2.60 | –1.42 | 6.73 | 0.08 | –1.88 | 0.15 |
| Elyana | 0.00 | 0.54 | 0.36 | 2.57 | –12.89 | –61.92 | 1.09 | 2.96 | 4.88 | –0.15 | –1.96 | –0.60 |
| FL 05-151 | –0.01 | 0.18 | 0.70 | –5.68 | –21.50 | –95.42 | 7.70 | –1.36 | –1.02 | 0.00 | –3.84 | –2.15 |
| Parental minimum | –0.06 | –1.05 | –3.09 | –5.80 | –44.48 | –95.42 | –7.08 | –5.70 | –10.01 | –0.15 | –3.84 | –2.15 |
| Parental mean | 0.00 | –0.12 | –0.17 | –1.29 | 0.78 | 8.66 | 0.76 | –1.24 | –0.02 | 0.01 | 0.04 | –0.04 |
| Parental maximum | 0.09 | 0.89 | 3.05 | 3.36 | 32.70 | 119.10 | 9.62 | 5.76 | 6.73 | 0.10 | 2.44 | 1.43 |
| Progeny minimum | –0.08 | –1.25 | –2.96 | –8.06 | –33.54 | –101.00 | –9.13 | –6.80 | –7.13 | –0.17 | –4.19 | –2.18 |
| Progeny mean | 0.00 | –0.25 | –0.58 | –0.46 | 6.68 | 21.82 | –0.97 | –0.69 | –0.20 | 0.00 | 0.40 | 0.24 |
| Progeny maximum | 0.10 | 1.12 | 3.56 | 15.38 | 40.39 | 172.40 | 12.89 | 14.55 | 7.53 | 0.12 | 4.22 | 2.10 |

[z]Fruit chemical traits include titratable acidity (TA), soluble solids content (SSC), and the SSC/TA ratio. Yield and fruit traits include average fruit weight (AWT), early marketable yield (EMY), total marketable yield (TMY), total cull fruit (TC), total misshapen fruit (TM), total water-damaged fruit (TWD), and fruit shape score (SHP). Vegetative traits are plant height (PHT) and total runners (TR). Parents are sorted in order of their breeding values for TMY from highest to lowest. Note that negative values for TC, TM, and TWD are desirable.

However, it is possible that increased yields in Florida above a certain point may saturate the market and lead to decreased prices. The potential consumer response to increased SSC has not yet been quantified.

Because of the narrow market window for Florida strawberry fruit and the fact that prices are highest early in the season, EMY is a trait of vital importance for the UF strawberry breeding program. Estimates of narrow-sense heritability ($h^2 = 0.18 \pm 0.07$) and broad-sense heritability ($H^2 = 0.39 \pm 0.04$) for EMY were low and moderate, respectively, suggesting that some gains can be made through breeding and selection and that genetic gains can be increased by twofold simply through clonal selection. EMY presented a positive high additive correlation ($0.54 \pm 0.21$) and genotypic correlation ($0.69 \pm 0.06$) with TMY, implying that many of the same genes control both traits and that the former trait may be used to some degree as a predictor of the latter for selection. In addition, these correlations were actually lower than those obtained from a smaller population in 2009–10 (unpublished data). The results obtained here are within the range of those reported by Shaw and Larson (2005) for early and total yield traits, $r_g = 0.52$ to $r_g = 0.82$ between 1999 and 2002. It should be mentioned that genetic parameters are specific to environments, and comparisons to other studies are made only to gain an appreciation for the potential genetic variation for the trait.

In the covariance analysis, the initial weight of the runner plants (measured before establishment) was found to be significant ($P < 0.05$) for PHT, EMY, and TMY. It is well known that the root mass and crown size of commercial nursery transplants impact their performance in the fruiting field and can be highly variable depending on cultural practices and environmental conditions. Based on field observations over several years, runner plant size within the breeding program summer nursery varies as a result of fluctuations in irrigation volume and soil drainage across the nursery. It also varies within genotype in that runners emerging earliest from the seedling mother plants root more quickly and reach a greater size by the time of harvest compared with those emerging later. Therefore, including the initial weight of each transplant in the analysis might improve the genetic parameter estimates by statistically accounting for environmental variability. Care must be taken, however, because it is possible that differences in runner plant weight may be partly under genetic control. The effect of such genetic variation on fruiting field traits would be obscured by including initial runner plant weight in the mixed model analysis. However, this did not seem to be the case because the inclusion of the covariate in the analyses either did not change or increased heritability estimates for EMY, TMY, and PHT. For EMY the addition of the covariate into the mixed model increased the estimates of $h^2$ and $H^2$ from 0.08 to 0.18 and 0.37 to 0.39, respectively.

Heritabilities of TMY and traits related to cull fruit such as TC, TM, and TWD were low to moderate ($H^2 = 0.30$ to $0.41$; $h^2 = 0.13$ to $0.23$) (Table 2). The heritabilities for TWD ($H^2 = 0.40 \pm 0.03$, $h^2 = 0.13 \pm 0.07$) were consistent with those estimated by Herrington et al. (2011) who found low narrow-sense ($h^2 = 0.20$) and moderate broad-sense ($H^2 = 0.49$) heritabilities for water damage resistance in a Queensland, Australia, strawberry seedling population. The authors described a laboratory soaking protocol that could improve the precision of phenotyping and thereby increase heritability estimates. TMY showed a high and negative genetic correlation with TC ($-0.72 \pm 0.17$) and with TM ($-0.59 \pm 0.23$) (Table 3). Interpretations of this result must

be made with caution because these correlations seem to reflect the mathematical connection between these two traits as they were calculated. The denominator of TC and TM includes the number of marketable fruit, which to some extent reveals information about TMY. It may be that the absolute values of the number of fruit in the different cull categories might better represent the genetic relationship between these traits, although these are, in practice, difficult to interpret.

Moderate and positive genetic correlations were found between TMY and the vegetative traits PHT ($0.58 \pm 0.20$) and TR ($0.50 \pm 0.25$) (Table 3); thus, additional increases are expected in these traits when selecting for greater yield. Practically speaking, runner production in the fruiting field is an undesirable trait because cutting runners involves labor costs for the grower. Larger plant sizes are also not desirable because large plants may obscure fruit and reduce picking efficiencies at current plant densities. Therefore, holding these traits at current levels may limit the potential rate of gain for yield on a per-plant basis.

## Conclusions

Genetic parameters for 12 commercially important strawberry traits were estimated for the UF strawberry breeding population using clonally replicated seedling genotypes from controlled crosses. Relationships among parents were accounted for using pedigree information spanning 15 generations. Moderate broad-sense heritabilities for most traits indicate that gains are possible for several economically important characters in the UF strawberry breeding population in terms of clonal deployment. Moderate to high narrow-sense heritabilities for AWT and PHT indicate a high probability of long-term gains through recurrent selection for these traits. All other traits exhibited low narrow-sense heritability estimates, indicating lower potential for gains over time, a situation that must be addressed in the breeding program. If these estimates are low as a result of experimental error in the field, greater numbers of clonal replicates, better experimental designs controlling spatial variation, and/or more frequent data collection could decrease the magnitude of non-genetic effects. If a lack of genetic diversity is constraining genetic variability for a given trait, infusion of unrelated germplasm may increase heritabilities by introducing new genes into the breeding population.

Strong and unfavorable genetic correlations exist for some pairs of traits, most notably for SSC and EMY, which must be considered when constructing a selection index. The discovery that using initial runner weight as a covariate improves the heritability of important traits such as EMY is significant because it will allow more accurate prediction of breeding values for these traits. A measure of caution should be taken in the interpretation of the genetic parameters from this study because they were derived from a single year and are potentially upwardly biased by $G \times Y$ interactions. Nevertheless, these parameters form an important basis for breeding decisions and will continue to be refined with additional data.

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