Predicted and Realized Response of Strawberry Production Traits to Selection in Differing Environments and Propagation Systems

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ABSTRACT. Strawberry (*Fragaria ×ananassa* Duch.) seedlings from a factorial mating design were tested in each of two locations using two propagule types (seedlings and runners). Genotypic correlations were used to indicate $G \times E$ interaction across these locations and propagation systems and to predict correlated responses between selection under specific conditions and commercial propagation. A combined index on relatives was constructed and used to select four groups of individuals—one for each location–propagule combination—for each of two production traits. Comparison was then made with realized responses from subsequent clonal testing at a single site representing the commercial environment. Although selection in the commercial environment (Watsonville) was predicted to give the greatest selection response, realized responses were greatest for the Wolfskill site. Additionally, the present system of selecting seedlings at Wolfskill and testing clones at Watsonville offers considerable logistical advantages that may outweigh genetic considerations. The concept of effective index heritability was introduced to enable the calculation of predicted response based on index selection. Neither the use of clonally tested parents nor a comparative seedling set selected for another trait was ideal for estimating realized response.

Breeding programs for many vegetatively propagated crops begin each cycle with an evaluation of seedlings generated from controlled crosses, followed by replicated testing of vegetatively propagated clones of selected individuals. For this testing procedure to succeed, the plant breeder must predict clonal performance reliably from that of the seedlings, although such testing can be complicated by differences in test environments or years. Different propagation systems and the test environment must be chosen based on relative selection efficiency—certain test environments or propagation systems may be more conducive to the separation of genetic effects from extraneous error than others. Additionally, interactions may occur between genetic response and specific environments ($G \times E$ interaction), including physiological features that may be conditioned by the propagation system itself.

The prediction of selection response from genetic tests conducted in different environments or established using different propagation methods uses genetic correlations and indirect selection theory. Most applications of indirect selection theory have been aimed at selecting one trait to obtain a correlated response in another on the same selection unit within the same environment. However, several studies (e.g., Burdon, 1977; Itoh and Yamada, 1990) have shown theoretically and empirically the value of using genetic correlations for predicting the correlated response of the same trait over different environments; genetic correlations were used as measures of $G \times E$ interactions and to indicate the reliability of predicted performance over environments, especially when conventional analyses of variance over environments were faced with constraints and unreasonable assumptions (Burdon, 1977). Validation of clonal performance from seedling data (Maris, 1988)

and prediction of juvenile–mature correlations (Lambeth, 1980) are other potential applications in clonally propagated crops. Genetic correlations can also be useful in characterizing those environments that would most efficiently screen seedling genotypes.

Such principles could apply to strawberry breeding programs. The strawberry breeding program based at the Univ. of California, Davis, has relied on propagating and evaluating seedlings at Wolfskill (near Davis) followed by testing runner-propagated clonal selections at Watsonville, among the commercial strawberry fields of the central Californian coast. The performance of strawberry genotypes at each of these locations is affected to a large extent by cultural and environmental factors (Voth and Bringham, 1962, 1970), and previous studies (Gooding et al., 1975; Shaw, 1989; Shaw et al., 1989) have shown the importance of genotype $\times$ location and genotype $\times$ propagation system interactions in strawberry. The aims of this study were to 1) predict the response to selection over environments that differed due to test site and propagation method and 2) compare predicted response with that realized in the subsequent testing of clonally propagated selections in one commercially realistic test environment. These results are then weighed against the practical implications of adopting the genetically optimal breeding strategy.

Materials and Methods

Yield trials were conducted at two research facilities of the Univ. of California: Watsonville (lat. 36° 56' N, long. 121° 46' W) and the Wolfskill experimental orchard (lat. 38° 32' N, long. 121° 58' W) near Davis. These two sites differ markedly in their seasonal and diurnal temperature patterns (Shaw, 1993); the Watsonville site is representative of semi-arid coastal sites typically used for commercial production. This experiment was conducted over two fruiting seasons. The first season (1990) involved measuring yield data from populations generated from a factorial crossing design

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Table 1. Trait means and standard errors (in parentheses) for the 1990 progeny populations with four site-propagule treatment combinations. Yield and fruit size data are in grams.

Site	Propagule	N	Yield	Fruit size
Wolfskill	Seedlings	318	852.3 (18.9)	16.5 (0.21)
	Runners	347	370.5 (11.0)	17.9 (0.21)
Watsonville	Seedlings	327	1460.4 (27.1)	17.7 (0.24)
	Runners	374	1267.8 (16.6)	20.4 (0.23)

(using runners and seedlings at both sites, thus giving four site-propagule combinations). The second season (1992) involved measuring selected individuals of the 1990 population as runner-propagated clones at Watsonville.

Response prediction, 1990

TRIAL DESIGN AND PROPAGATION METHODS. A 5×4 factorial crossing design among nine parents from the California strawberry improvement program was used in this study. Parents were chosen based on good overall performance for a number of traits, having been tested as clones over a number of preceding seasons, but were otherwise a random sample of available advanced selections. The assumption of unrelatedness of parents is probably valid for this population, as inbreeding coefficients based on their pedigrees were small and had accumulated over several generations with intervening cycles of selection based on clonal performance (Shaw, 1995).

Two types of propagation methods were used for all families at each site: seedlings (18 families used) and clonal runners from seedlings (all 20 families used). Plants to be tested as seedlings at both sites were raised at Davis in June 1989, and 20 randomly chosen individuals were planted out directly to each of two sites in September 1989. There were 20 genetically different individuals representing each family at Wolfskill, with a different set of 20 genotypes representing each family at Watsonville.

For those plants destined for testing as runners for each site, 20 randomly chosen seedlings from each family were raised at Davis as above, with germination beginning earlier (April 1989). Each of these seedlings was planted in a nursery at Wolfskill in June 1989 to produce runners, four of which were harvested from each seedling genotype on 27 Oct. to be stored at 2°C until planting in early November 1989. Thus, only 20 genotypes were raised per family, with four runners cloned from each original seedling genotype and distributed to each site (two for Wolfskill, two for Watsonville).

Both sites were planted in a randomized complete-block (RCB) design. For the seedlings, there were two replications per site, with a single plot of 10 genotypes in each replication. To facilitate randomization within the runner plants, the 20 genotypes from each full-sib family were further distributed between two plots within each replication, each plot containing 10 genotypes. Further details of plot layout are given in Shaw (1993). Data from the two runners of each genotype planted at each site were averaged before data analysis. Data loss due to plant mortality and nonyielding types left the sample numbers given in Table 1.

TRAIT MEASUREMENT AND SELECTION. Fruit harvesting began in April 1990 at each site and continued for 12 consecutive weeks at Wolfskill and for 16 weeks at Watsonville. These were only part-season records, being summarized early enough to enable the

selection of genotypes to be propagated by runners in time for their subsequent nursery propagation and clonal evaluation at Watsonville in 1992. Records were taken on an individual plant basis. Yield was measured as total cumulative fruit mass on a per plant basis, fruit size was calculated from total yield and fruit number over the harvest season. Extreme outliers were omitted before analysis, and no transformation of the raw data was required.

Selection was performed using an index on relatives for each trait separately (see below), based on the data obtained from the four site-propagule trials measured in 1990. Ten genotypes were selected within each of the four site-propagule combinations for their superior fruit size and ten were likewise selected for superior yield, giving, in total, eighty selected individuals.

ESTIMATION OF GENETIC PARAMETERS. Model variance components and coefficients were estimated from the SAS GLM procedure (SAS Institute Inc., Cary, N.C.) using Type III sums of squares and the linear model defined in Table 2 (Searle, 1971), with replications treated as a fixed effect. The error term used in these analyses equates to the within-family genetic variance plus all environmental variation. This pooled error term was used to enable direct comparison among the four site-propagule treatments. Each site-propagule combination was analyzed separately. Translation of model variance components to causal components follows Hallauer and Miranda (1988):

$\sigma_A^2 = 2(\sigma_r^2 + \sigma_m^2)$ [alternatively $4\sigma_r^2$ or $4\sigma_m^2$ if any source variances are negative]

$\sigma_D^2 = 4\sigma_{fm}^2$

where σ_A^2 and σ_D^2 are the variances due to additive and dominance genetic effects respectively. Assumptions necessary for this translation have been discussed previously (Comstock et al., 1958; Shaw, 1990). Heritability estimates for full-sib (FS) families ($h^2_{FS(c)}$) and within-family deviations (h^2_w) appropriate to subse-

Table 2. Expected mean squares (EMS) and degrees of freedom (df) for Type III sums of squares analysis of variance of the factorial design used in this study.

Source	df	EMS ^a
Replications (R)	See below	$\sigma_e^2 + k_r \sigma_r^2$
Females (F)	4	$\sigma_e^2 + k_f \sigma_{mf}^2 + k_3 \sigma_f^2$
Males (M)	3	$\sigma_e^2 + k_m \sigma_{mf}^2 + k_2 \sigma_m^2$
F $\times$ M	See below	$\sigma_e^2 + k_{fm} \sigma_{fm}^2$
Error	See below	σ_e^2

Values of k and df for each set considered separately as follows:

	Wolfskill		Watsonville	
	Seedlings	Runners	Seedlings	Runners
df				
Replications	1	---	1	---
F $\times$ M	10	12	10	12
Error	299	327	308	354
Coefficients (k)				
k_1	17.4	17.1	17.9	18.5
k_2	73.7	83.3	76.6	89.8
k_3	60.0	67.0	61.9	71.9
k_4	158.2	---	157.0	---

^a σ_r^2 = variance due to replications; σ_f^2 , σ_m^2 = variance due to females and males, respectively; σ_{fm}^2 = variance due to female $\times$ male interaction; σ_e^2 = pooled residual variance (see text); r, m, f, and k = number of replications, males, females, and individuals respectively.

quent clonal propagation were calculated as follows:

$$h_{FS(c)}^2 = [1/2\sigma_A^2 + 1/4\sigma_D^2] / [1/2\sigma_A^2 + 1/4\sigma_D^2 + \sigma_e^2/n]$$

$$h_W^2 = [1/2\sigma_A^2 + 3/4\sigma_D^2] / \sigma_e^2$$

where σ_e^2 is the within-family genetic variance plus all environmental variation (Table 2), and n is the mean number of individuals per family. Epistatic sources of variance were assumed to be insignificant (Shaw, 1990) and have been ignored for analysis purposes. Standard errors of these heritability estimates were calculated as follows:

$$SE(h_{FS(c)}^2) = [1/4SE(\sigma_A^2) + 1/16SE(\sigma_D^2)] / [1/2\sigma_A^2 + 1/4\sigma_D^2 + \sigma_e^2/n]$$

$$SE(h_W^2) = [1/4SE(\sigma_A^2) + 9/16SE(\sigma_D^2)] / \sigma_e^2$$

A combined selection index (I) for each individual, based on relatives, was calculated separately for each trait and for each set of site-propagule combinations following Van Vleck (1983):

$$I = h_{FS(c)}^2 X_{fam} + h_W^2 X_{ind}$$

where X_{fam} is the family mean and X_{ind} is the deviation of each individual from its family mean. Individuals with the top ten index values from each of the four site-propagule combinations were retained, with one set selected based on yield and another based on fruit size. Yield and fruit size data were available for each selected set.

Genotypic correlations (r_{Gxy}) between yield (x) and fruit size (y) among individuals of the same site-propagule combination (used for Table 4) were calculated following Falconer (1989):

$$r_{Gxy} = \text{cov}_{Gxy} / \sqrt{(\sigma_{Gx}^2 \sigma_{Gy}^2)}$$

Covariances were estimated using the SAS procedure GLM and MANOVA statement with the same model as that given for the ANOVA above (Table 2). Cov_{Gxy} was calculated from the analysis of cross products as follows:

$$\text{cov}_{Gxy} = \text{cov}_{Axy} + \text{cov}_{Dxy}$$

$$= 2(\text{cov}_f + \text{cov}_m) + 4\text{cov}_{fm}$$

Genotypic correlation coefficients (r_{Gxy}) between pairs of site-propagule combinations for each trait (used for Table 5) were estimated from the phenotypic product-moment correlations (r_{Pxy}) between family means as follows (Burdon, 1977):

$$r_{Gxy} = r_{Pxy} / [h_{FS(c)x} h_{FS(c)y}]$$

where $h_{FS(c)x}$ and $h_{FS(c)y}$ are the square roots of the heritabilities for the site-propagule combinations for traits x and y respectively.

The direct response to combined index selection (R_{Iy}) was predicted for the Watsonville runners (y) following Van Vleck (1983):

$$R_{Iy} = i_y [h_{FS(c)}^2 (1/2\sigma_A^2 + 1/4\sigma_D^2) + h_W^2 (1/2\sigma_A^2 + 3/4\sigma_D^2)]^{1/2}$$

where i is the selection intensity.

Genotypic correlations were used to calculate predicted correlated response ($CR_{y/x}$) for each trait from each original site-propagule combination (x) to clonal testing as runners at Watsonville (y):

$$CR_{y/x} = i_x r_{Gxy} (h_x^2 h_{y \text{ eff}}^2)^{1/2} \sigma_{Py}$$

where σ_{Py} is the phenotypic standard deviation of trait y . For the prediction of Watsonville clonal performance from individuals selected from the Watsonville runner population, the above equation reduces to calculation of direct response (R_{Iy}). As heritability estimates cannot be calculated directly when combined index selection has been practised (Falconer, 1989), effective index heritabilities ($h_{y \text{ eff}}^2$), to be used in the estimation of correlated

response, were calculated as

$$h_{y \text{ eff}}^2 = R_{Iy} / S_y$$

where R_{Iy} is the response predicted for index selection and S_y is the selection differential, or difference between the original and selected population means, for each trait at each site based on the raw data.

Realized response, 1992 season

The 80 selected individuals were propagated by runners in an outdoor nursery at the Wolfskill experimental location according to standard practices (Welch, 1989) and planted in November 1991 in a RCB design at Watsonville only. Realized response trials were established with two replications per selection and a single plot of ten runners per selection in each replication. Yield and fruit size data were collected from all plots throughout the complete season (April to September 1992).

Realized response was calculated (per trait) as the mean performance of the selections from the original site-propagule groups, propagated as runners at Watsonville in 1992, from which was subtracted the mean values for the group of genotypes selected for the other trait from the same original site-propagule population. The use of this unselected population, as opposed to parental clones, as a control for the calculation of realized response will be mentioned in the discussion.

Results

Descriptive statistics for the progeny populations evaluated in 1990 are given in Table 1. Generally, the Watsonville populations performed better than their respective Wolfskill counterparts for yield (1268 and 1460 g vs. 371 and 852 g) and fruit size (17.7 and 20.4 g vs. 16.5 and 17.9 g). At both sites, the runners had lower yields but larger mean fruit sizes than the corresponding seedlings. Coefficients of variation for the progeny populations varied from 0.25 to 0.55 for yield, but were consistent (range 0.22 to 0.25) across site-propagule combinations for fruit size, the latter being similar to those reported earlier for seedling populations at each site (Shaw et al., 1989).

Genetic variance components for both traits varied in magnitude (for yield $\sigma_A^2 = 0$ to 55426, $\sigma_D^2 = 1799$ to 52754; for fruit size $\sigma_A^2 = 1.47$ to 15.41, $\sigma_D^2 = 0$ to 3.97) and showed no clear pattern with respect to site or propagule type (Table 3). Full-sib family heritability estimates for fruit size were generally higher than those for yield for each respective site-propagule combination, with a range of ratios from 0.53 to 0.92. Also, heritabilities estimated for the Watsonville populations were generally higher than those for Wolfskill, and heritabilities for populations propagated as runners were generally higher than for seedlings (yield for the Wolfskill seedling population was the only exception).

Table 4 shows the genotypic (r_G) and phenotypic (Pearson product-moment, r_P) correlations between yield and fruit size, calculated from individual plant data for each site-propagule combination separately. Phenotypic correlations between these traits were near zero ($r_P = -0.005$) for Wolfskill and only slightly higher at Watsonville ($r_P = 0.153$ to 0.268). Genotypic correlations were all moderate in magnitude, but that for Wolfskill runners differed in sign compared to the other populations (-0.574 vs. 0.431 to 0.642). Thus, for all but the Wolfskill runners, genotypic selection for one trait is expected to result in a positive correlated response in the other.

Phenotypic correlations of family trait means were uniformly positive but nonsignificant for all paired yield estimates, but both

Table 3. Mean squares and estimates of genetic parameters derived from the ANOVA of the 1990 progeny data. All variance components are in units of square grams.

Source	Yield				Fruit size			
	Wolfskill		Watsonville		Wolfskill		Watsonville	
	Seedling	Runner	Seedling	Runner	Seedling	Runner	Seedling	Runner
Reps	183808	---	1120796**	---	12.8	---	101.8**	---
Females(F)	231107	93162	1028323**	91941	50.4**	98.5**	63.5**	103.4**
Males (M)	109365	182324**	1666526**	611831**	46.7**	178.4**	308.1**	599.5**
F × M	273890**	47846	364570	333146**	24.4	11.4	33.4*	16.2
Error	106525	40147	213026	89761	13.1	13.5	15.6	12.8
$\sigma^2_{A_2}$	0 ²	4580	55426	12407	1.47	6.61	8.15	15.41
$\sigma^2_{D_2}$	38577	1799	33841	52754	2.60	0 ²	3.97	0.75
$h^2_{FS(c)}$	0.61	0.53	0.75	0.80	0.65	0.80	0.85	0.92
SE	0.22	0.28	0.26	0.21	0.25	0.30	0.30	0.36
h^2_w	0.27	0.09	0.25	0.51	0.21	0.22	0.45	0.65
SE	0.15	0.09	0.13	0.21	0.12	0.13	0.20	0.30

²Empirically was small and negative, therefore equated to zero for subsequent calculations.

*, **Significant at $P = 0.05$ or 0.01 , respectively.

Table 4. Estimates of genotypic ($r_{G_{xy}}$) and Pearson product-moment (r_T) correlation coefficients between yield and fruit size in 1990 for each site-propagule combination.

Site	Propagule	$r_{G_{xy}}$	r_T
Wolfskill	Seedlings	0.522*	-0.005
	Runners	-0.574**	-0.005
Watsonville	Seedlings	0.642**	0.153
	Runners	0.431	0.268

*, **Significant at $P = 0.05$ or 0.01 , respectively.

were positive and highly significant for all cross-site comparisons of fruit size (Table 5). Genotypic correlations for fruit size, among sites and propagule types, were high ($r_G = 0.778$ to 0.974), but such correlations were low to moderate for yield ($r_G = 0.072$ to 0.478). The genotypic correlations for yield from the present system of evaluating seedlings at Wolfskill and yield obtained through clonal testing at Watsonville was especially low ($r_G = 0.072$), suggesting this may not be the most efficient selection strategy for improving this trait.

Descriptive performance statistics obtained for the selections propagated by runners and tested in 1992 at Watsonville are summarized in Table 6. For all site-propagule combinations, those retained for yield had higher yields as clones at Watsonville than those retained for fruit size. The same was true when fruit size selection was practiced. The runner selections retained for fruit size had larger fruit than corresponding seedling selections at each

site when tested in 1992. This trend was not as clear when yield comparisons were made; Wolfskill seedling selections and Watsonville runner selections retained in 1990 for yield had the highest yields when evaluated as runners in 1992 at Watsonville.

Predicted responses for yield and fruit size were greatest for the Watsonville runners and least for the Wolfskill seedlings (Table 7). Assuming the same selection intensity for all options, no site-propagule combination was as effective in predicting (correlated) selection response as direct selection at Watsonville using runners (i.e., $r_{G_i} \cdot h_{x,eff} < h_{y,eff}$), despite significant genotypic correlations between fruit size and yield for Wolfskill seedlings and between Wolfskill seedlings and Watsonville runners for fruit size. In fact, minimal response was predicted for yield when selection was performed at Wolfskill. Generally, runners showed greater predicted responses than seedlings at the same site, and predicted response for selections made at Watsonville was larger than for Wolfskill for both propagule types.

Realized selection responses differed slightly in pattern from absolute trait values due to small differences in selection intensities applied to the four original populations (Table 7). For yield, realized response was greater than predicted for populations evaluated at Wolfskill, and very close to predicted values for populations evaluated at Watsonville. Overall, selection for each character was effective for all site-propagule combinations in the sense that performance of the selected group was superior to the equivalent unselected group (i.e., selected for the alternate trait).

Table 5. Estimates of family-mean phenotypic (above each diagonal) and genotypic ($r_{G_{xy}}$, below each diagonal) correlation coefficients between sites and propagule types for the two traits of interest (1990 data).

Trait	Site	Propagule	Wolfskill		Watsonville	
			Seedlings	Runners	Seedlings	Runners
Yield	Wolfskill	Seedlings	---	0.171	0.207	0.050
		Runners	0.301	---	0.287	0.154
	Watsonville	Seedlings	0.321	0.478	---	0.233
		Runners	0.072	0.237	0.316	---
Fruit size	Wolfskill	Seedlings	---	0.671**	0.604**	0.602**
		Runners	0.931	---	0.803**	0.822**
	Watsonville	Seedlings	0.813	0.974	---	0.794**
		Runners	0.778	0.958	0.898	---

**Significant at $P = 0.01$.

Table 6. Means and their standard errors (in parentheses) of the 1990 selections, tested at Watsonville in 1992 as runners. All figures are in units of grams. Standard errors are in parentheses.

Site	Propagule	Selections retained for yield		Selections retained for fruit size	
		Yield	Fruit size	Yield	Fruit size
Wolfskill	Seedlings	1915 (246)	20.94 (0.49)	1459 (189)	23.38 (0.90)
	Runners	1774 (126)	21.74 (0.43)	1483 (129)	26.70 (0.57)
Watsonville	Seedlings	1484 (115)	21.94 (0.75)	1342 (104)	24.73 (1.47)
	Runners	1957 (167)	23.87 (0.34)	1594 (99)	27.15 (0.57)

Discussion

Selection for each trait resulted in positive realized responses irrespective of site and propagule type. However, neither their patterns nor their absolute values followed those for predicted responses closely. For example, realized responses for fruit size averaged 63% of those predicted; average response for yield was somewhat larger than predicted, but selections from both Wolfskill populations exceeded expectations substantially. In fact, the greatest realized response to yield selection was from those selected from Wolfskill as seedlings, even though predicted response was lowest for this group (Tables 6 and 7). Such discrepancies may arise from errors of estimation for the parameter used for prediction, measurement error in the testing of realized response, peculiarities of performance with this site-propagule combination that were unable to be defined, or the failure of one or more assumptions of the model itself. Because both genetic parameter estimates and response predictions have large sampling errors (Sales and Hill, 1976), systematic errors due to violated assumptions will be difficult to separate from sampling error in our experiment. Also, predicted responses were calculated from only one year's data; year effects may be important.

Irrespective of site, greater gain was predicted from runner-propagated genotypes. This is not unexpected as the use of clones would be expected to predict subsequent clonal performance better by pooling of the environmental variation. In reality, realized responses for yield and fruit size were greater for selections based on runners, the exception being yield response for the Wolfskill runners. Given the genotypic correlations in Table 4, realized responses for yield as presented in Table 7 may be lower than expected for all but the Wolfskill runner population; Wolfskill seedlings and Watsonville runner populations could be expected to have greater yields than were found.

From a practical perspective, selection using information from runners tested at the intended production site, Watsonville, resulted in advanced populations with the largest mean values for yield and fruit size. For fruit size, selection intensities for the four populations (Table 7) differed by 10% at most (2.120 to 2.348), and could have contributed little to differences among these observed population means. For yield, the range of selection intensities was larger (1.736 to 2.578), making direct comparison of selected population means more difficult. However, differences in selection intensity fail to explain the observation that selected population means for items retained from the Wolfskill seedlings and the Watsonville runners were nearly identical. Thus, although the present system of evaluating seedlings at Wolfskill is predicted to be genetically the least efficient for obtaining selection response for fruit size and yield, performance of runner-propagated clones of selections from these sources at Watsonville differed little.

One limitation of using selections chosen for the alternate trait as a control group for estimating realized response is that yield and fruit size are not genetically independent. Genotypic correlations between the traits (Table 4) are expected to cause a correlated response when selecting for the other trait. For positive correlations, estimates of realized selection response will thus be biased downward, and vice versa for negative correlations. This expectation is consistent with realized responses greater than expected for both traits in selected items from Wolfskill runners; however, it does not explain the unexpected success of the selection for yield from the Wolfskill seedling population. The observation that genetic correlations change in sign between the site-propagule combinations may indicate complex interactions and reflect assumptions violated by our relatively simple models. Using parental clones as an alternative for the control in the estimation of realized response also has drawbacks: such genotypes have been selected over several clonal generations and as such represent

Table 7. Selection intensity (i), effective heritability (h^2_{eff}), predicted response (R_p), and realized response (R_R) to selection for each site and propagule type, for the two traits of interest. Units of measurement for response is in grams. Note that the response predicted for the Watsonville runners is calculated as a direct response, R_{ly} , whereas all others reflect correlated response ($CR_{y/x}$) (see text).

Site	Propagule	Yield				Fruit size			
		Selections retained for yield				Selections retained for fruit size			
		i	h^2_{eff}	R_p	R_R	i	h^2_{eff}	R_p	R_R
Wolfskill	Seedlings	2.166	0.35	25	456	2.327	0.32	3.47	2.44
	Runners	2.578	0.21	45	291	2.169	0.46	5.09	4.96
Watsonville	Seedlings	1.736	0.41	136	143	2.120	0.62	5.98	2.79
	Runners	2.409	0.62	475	363	2.348	0.81	8.35	3.28

individuals selected over a range of environments (years). Their performance in any one year would therefore be expected to exceed those genotypes selected after 1 year's performance data. A set of seedlings not selected for any trait was not available for use as a control.

Heritabilities cannot be calculated directly when an index is used for selection. This is because of the combined use of different sets of information in construction of the index, in this case the use of weighted family and individual information for the same trait. An effective index heritability was thus calculated retrospectively using the gain equation after the response had been predicted (R_{I_y}) with variance components and appropriate full-sib and within family heritabilities. One estimation of heritability for index selection was thus determined.

The practice of using clones for the initial screening of genotypes, as well as for obtaining genetic information such as epistatic effects, has been investigated in theory and in practice for several crops (Burdon and Shellbourne, 1974; Foster and Shaw, 1988; Maris, 1986, 1988; Shaw and Hood, 1985). Although increased gains can be made using clones, it depends on the mode of selection, given similar test effort. Importantly, the use of as few as two runners per genotype (as in our study) doubles the effort required to evaluate the progeny population, a consideration when >10,000 genotypes per year are usually evaluated. Other factors such as increased cycle time for systems that require the propagation of runners, differences between sites for pest and disease incidence, and simple logistics must be considered as well.

Whatever the relative merits of genetic and logistical considerations are, the main outcome required of seedling evaluation among individuals would be to avoid missing or excluding any potentially useful genotypes. Providing selection intensities are not too high, subsequent clonal testing over multiple seasons without recombination should be sufficient to capture the best performers. This is particularly important in strawberries, a crop that seems especially responsive to the environment.

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