Phenotypic, Genotypic, and Environmental Correlations in Sweet Potatoes[1]

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Abstract. Estimates of phenotypic, genotypic and environmental correlations of 21 sweetpotato traits indicated no serious impediments to selection for improved horticultural types through mass selection techniques. Some secondary traits were genetically correlated with traits of primary economic importance, a factor which suggests that their use in selection indices may be profitable in sweetpotato improvement programs.

VARIANCE and covariance components estimated from a parent-offspring study of sweet potatoes, *Ipomoea batatas* (L.) Lam., led to rather high heritability (h^2) estimates for wilt resistance (3), 10 root traits (5), and 10 vine traits (4). Realized gains from mass selection fit expectations well, indicating that the estimates were reasonable. Root traits of most economic importance tended to have lower h^2 estimates than either vine traits or those root traits of less economic importance. Although favorable gains from mass selection were possible for each of the 21 characters studied, gains from simultaneous selection for more than one character would depend on the associations of the various traits. Therefore, effective application of results from the above studies depends on a knowledge of character correlations. The purpose of this paper is to present estimates of phenotypic, genotypic and environmental correlations of the 21 traits previously reported (3, 4, 5).

MATERIALS AND METHODS

Data of 20 traits (Table 1) were collected from 40 parent clones and their respective open-pollinated offspring in a test replicated 3 times and grown under 6 environments (2 years at 3 locations) as previously described (4, 5). One trait, wilt resistance, was studied under only 2 environments and all estimates involving it were limited to those two environments (3). Correlations were obtained by procedures as outlined by Falconer (1, chapter 19). Phenotypic correlations (r_p) of pairs of traits were estimated from data for parent clones. Genotypic correlations (r_G) of pairs of traits were computed as:

$$r_G = \frac{\text{Cov. xy}}{\sqrt{\text{Cov. xx. Cov. yy}}}$$

Table 1. Methods of scoring individual sweet potato plants for 21 traits. All analyses were conducted on 5 plant plot totals.

Trait	Method	Units	Notes
Wilt index	Subjective	0–20	Increasing susceptibility to *Fusarium oxysporium* Schlecht. f. sp. *batatas* (Wr.) Snyd. and Hans.
Root weight	Weight	lbs.	Nearest tenth
No. edible roots	Count	No.	Enlarged roots
Root veining	Subjective	1– 4	Increasing expression
Root growth cracks	Subjective	1– 4	Increasing expression
Root flesh oxidation	Subjective	1– 5	Increasing discoloration after 10 min. with 0.25 molar solution of catechol
Root shape	Subjective	1– 5	Long and irregular, fusiform long, fusiform short, short and chunky, round
Root flesh color	Subjective	1– 5	White, cream, salmon, orange, dark orange
Root cortex thickness	Measure	mm	Enlarged root portions
Root skin color	Color standards	1–25	U. S. Department of Agriculture, color fan for sweetpotato skin
Root skin purpling	Code	1–10	From above for increasing degrees of purple (2)
Leaf vein purpling	Subjective	1– 6	Increasing expression
Buds per cyme	Count	No.	Maximum
Leaf whorl purpling	Subjective	1– 5	Increasing expression
Vine purpling	Subjective	1– 5	Increasing expression
Vine diameter	Code	1– 6	Stem diameter gauge, increasing size at fourth or fifth node from tip
Vine length	Measure	Feet	Nearest foot
Internode length	Measure	cm	At fourth or fifth node from tip
Leaf length	Measure	cm	Mature leaves
Plant pubescence	Subjective	1– 5	Increasing expression
Leaf type	Subjective	1– 3	Entire to deeply lobed (2)

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where Cov. xy is the cross-covariance (parental value for trait x times the respective offspring value for trait y) and Cov. xx and Cov. yy are the respective parent-offspring covariances previously computed (3, 4, 5). Environmental correlations (r_E) of pairs of traits were obtained from the following formula:

$$r_p = h_x h_y r_G + e_x e_y r_E$$

when h_x and h_y are square roots of heritabilities (3, 4, 5) for traits x and y respectively and e_x and e_y are:

$$e_x = \sqrt{1\text{-}h^2_x} \text{ and } e_y = \sqrt{1\text{-}h^2_y}.$$

The phenotypic covariances of pairs of characters and the cross-covariances of pairs of characters were obtained by using forms of analyses like those used in obtaining estimates of genetic components of variance (4, 5).

Because the cross-covariance can be computed in 2 ways (x parents times y offspring or y parents times x offspring) 2 estimates each of r_G and r_E were provided for each pair of traits. To test whether the 2 estimates of a given correlation were different, the procedure outlined by Snedecor (7, pg 151) was used. If the 2 r_G estimates were not different at the .01 level of probability, they were averaged. The estimates of r_p, r_G and r_E were subjected to a test of the null hypothesis as outlined by Snedecor (7, pg 149) with $n = 40$. Only those pairs of traits with significant r_p or r_G estimates are presented in this paper.

When h^2 estimates were very high, the e_x and e_y values were so small that resulting r_E estimates were anomalous. For this reason r_E was not computed when either one or both of the traits involved had a h^2 estimate above .95.

Table 2. Correlations for pairs of traits for which the 2 estimates of r_G were averaged, and r_E was computed.[a]

Traits			Correlations[b]		
			Phenotypic (r_p)	Genotypic (r_G)	Environmental (r_E)
Wilt index	x	root weight	−.14	−.57**	.70**
	x	no. edible roots	−.11	−.45**	.40**
	x	root flesh color	−.19	−.47**	.74**
	x	root skin color	−.30	−.54**	.91**
	x	root skin purpling	−.33*	−.53**	.48**
	x	leaf whorl purpling	.26	.32*	.00
	x	vine purpling	.24	.31*	.11
Root weight	x	no. edible roots	.88**	.89**	.88**
	x	root growth cracks	.35*	.14	.54**
	x	root flesh oxidation	−.23	−.45**	.00
	x	root shape	.50**	.39*	.63**
	x	root flesh color	.22	.45**	−.03
	x	root cortex thickness	.23	.37*	.12
	x	plant pubescence	.31*	.00	.95**
No. edible roots	x	root growth cracks	.32*	−.10	.63**
	x	root flesh oxidation	−.31*	−.55**	−.11
	x	root shape	.57**	.34*	.79**
	x	root flesh color	.26	.51**	.06
	x	root skin color	.03	.57**	−.73**
	x	leaf whorl purpling	−.10	−.31*	.12
Root veining	x	buds per cyme	−.27	−.34*	−.23
Root growth cracks	x	root shape	.43**	.45**	.42**
	x	root cortex thickness	−.31*	−.17	−.44**
	x	root skin purpling	−.33*	−.29	.00
	x	buds per cyme	−.17	−.39*	.05
	x	vine length	.20	.32*	.05
Root flesh oxidation	x	root flesh color	−.88**	−.88**	−.87**
	x	leaf whorl purpling	.32*	.18	.62**
	x	vine purpling	.23	.48**	−.11
Root shape	x	buds per cyme	−.06	.33*	.28
	x	vine length	.30	.50**	−.01
	x	internode length	.28	.49**	−.05
Root flesh color	x	leaf whorl purpling	−.32*	−.22	−.56**
	x	vine purpling	−.26	−.40**	−.04
	x	leaf type	−.21	−.34*	.01
Root cortex thickness	x	root skin color	.39*	.45**	.18
	x	root skin purpling	.39*	.45**	.21
Root skin color	x	root skin purpling	.95**	.98**	.86**
Buds per cyme	x	leaf whorl purpling	−.36*	−.32*	−.46**
Leaf whorl purpling	x	vine purpling	.46**	.38*	.62**
Vine purpling	x	leaf type	.30	.39*	.17
Vine length	x	internode length	.94**	.97**	.90**

[a] Only those pairs of traits with r_p, r_G or both of significance are listed.

[b] Correlations marked * are significant at 5%; those marked **, at 1%.

RESULTS AND DISCUSSION

For those pairs of traits where the 2 estimates of r_G could be averaged, significant r_p and r_G estimates are given in Table 2 with their respective r_E estimates. Significant r_p and r_G estimates involving characters with h^2 above .95 are presented in Table 3. Those pairs of traits for which 2 different estimates of r_G were obtained are presented in Table 4.

It is interesting that pairs of traits often have no phenotypic correlation but are correlated genotypically, sometimes with an environmental correlation of opposite sign. When this is the case, the genotypic and environmental sources of variation may affect the characters through different physiological mechanisms. For instance, wilt index and root weight have a sizable negative r_G which is offset by a positive r_E, such that r_p is negligible (Table 2). These correlations may indicate that plants with heavy roots due to genetic endowment tended to have progeny with low wilt indices (resistance) while plants with heavy roots due to environmental causes tended to have progeny with high wilt indices. Or, those environmental sources of variance responsible for high root weight were also responsible for reduced wilt resistance. These interpretations may have some bias, since the method of estimating r_E included correlations due to non-additive genetic causes.

Root weight is known to have an important non-additive genetic component (5) while that of wilt resistance is negligible (3). Perhaps the non-additive component of root weight is correlated with wilt resistance in an opposite manner to that of the additive component. One could theorize a non-additive component of root weight expressed as differential plant vigor. An increase in plant vigor due to the non-additive component could cause more succulent vine tips and, thus, a tendency to appear more susceptible in greenhouse wilt tests. Reduced vigor could cause less succulent vine tips and an apparent increase in resistance in greenhouse tests. Reaction to increased vigor under field conditions could be the very

Table 3. Correlations for pairs of traits for which the 2 estimates of r_G were averaged but estimates of r_E were not appropriate because one or both traits had heritability estimates of .95 or above.[a]

Traits			Correlations[b]	
			Phenotypic (r_p)	Genotypic (r_G)
Root weight.........	x	leaf vein purpling	.41**	.45**
No. edible roots......	x	leaf vein purpling	.40**	.53**
Root growth cracks...	x	leaf length	–.29	–.53**
Root shape..........	x	vine diameter	–.02	–.34*
	x	leaf length	–.07	–.33*
Root flesh color......	x	vine diameter	.39*	.39*
Root cortex thickness.	x	vine diameter	–.11	–.40**
Leaf vein purpling...	x	vine purpling	.51**	.42**
	x	leaf length	.34*	.32*
	x	leaf type	.45**	.58**
Buds per cyme.......	x	vine diameter	.26	.40**
Leaf whorl purpling..	x	vine diameter	–.23	–.41**
Vine diameter.......	x	vine length	–.26	–.32*
	x	internode length	–.36*	–.43**
	x	leaf length	.61**	.73**
	x	plant pubescence	.44**	.46**
Internode length.....	x	leaf length	–.26	–.32*
Leaf length.........	x	plant pubescence	.41**	.22
	x	leaf type	.31*	.42**

[a] Only pairs of traits with r_p, r_G or both of significance are listed.
[b] Correlations marked * are significant at 5%; those marked **, at 1%.

Table 4. Correlations for pairs of traits for which the 2 estimates of r_G could not be averaged and for which there were 2 estimates of r_E.

Traits			Correlations[a,b]				
x		y	Phenotypic (r_p)	Genotypic (r_G)		Environmental (r_E)	
				xy	yx	xy	yx
Wilt index	x	root veining	.24	.16	1.03**	.51**	–.85**
	x	buds per cyme	.06	.55**	–.16	1.13**	.62**
Root weight	x	root skin color	.08	.19	.67**	–.08	–.90**
	x	root skin purpling	–.01	.07	.61**	–.13	–.89**
	x	vine length	.29	.23	.72**	.37*	–.13
	x	internode length	.29	.20	.67**	.40**	–.09
No. edible roots	x	root skin purpling	–.04	.19	.79**	–.32*	–1.01**
	x	vine length	.19	.01	.57**	.36*	–.11
	x	internode length	.15	–.03	.64**	.33*	–.25
Root veining	x	root growth cracks	–.23	–.67**	–.18	.04	–.28
	x	leaf vein purpling[c]	–.16	–.14	.58**	—	—
	x	flesh oxidation	.04	–.18	.43**	.24	–.29
	x	vine length	–.19	–.43**	.32*	–.01	–.61**
	x	internode length	.00	–.26	.41**	.20	–.34**
	x	leaf length[c]	.24	.59**	–.03	—	—
	x	plant pubescence	.27	.57**	.03	–.03	.72**
	x	leaf type	.03	.67**	.18	–.46**	–.08
Root growth cracks	x	plant pubescence	–.21	–.75**	–.17	.93**	–.32*
Root flesh color	x	buds per cyme	.13	.36*	–.22	–.18	.62**
Root skin purpling	x	buds per cyme	.05	.05	.61**	.06	–.90**
Vine purpling	x	plant pubescence	.12	–.34*	.27	1.17**	–.20

[a] The first trait indicated (x or y) was from the parent clone and the second trait (y or x) from the offspring as explained for cross-covariances in materials and methods section of the text.
[b] Correlations marked * are significant at 5%; those marked **, at 1%.
[c] Because of the high h^2 of trait y, r_E was not computed.

opposite with high vigor contributing to increased resistance. Such reasoning may explain why some plants appear consistently more resistant in the field than the greenhouse wilt tests indicate. Application of such reasoning to breeding programs would suggest that breeding potential for wilt resistance should be based on greenhouse tests, but that varietal potential may best be determined under field conditions.

In some instances, such as root weight and number of edible roots, the environmental correlation reinforced the genotypic correlation and the phenotypic correlation was large. In other instances, a significant r_p was accounted for by a large r_E as found for root weight and growth cracks. Selection for either trait should have no affect on the other, even though r_p is significant.

Selection for wilt resistance would not be expected to adversely affect any of the other traits of horticultural value studied. Although no large r_p was observed, the r_G estimates suggest that selection for wilt resistance would result in increased root weight, more edible roots, more orange flesh types, darker skin colors, and perhaps less leaf whorl and vine purpling. Selection for an increased number of edible roots, or reduced root flesh oxidation, or increased carotene would not have any adverse side effects relative to the traits in this study.

Root weight is of primary importance, and thus associations with it are of particular interest. No adverse correlations were found and selection for high root weight might increase resistance to wilt, increase the number of edible roots per hill, decrease the degree of root flesh oxidation, increase the diameter or roots relative to their lengths, increase the frequency of orange flesh types; and perhaps increase the thickness of the root cortex. Apparent correlations (r_p) with growth cracks and plant pubescence are due to r_E; and selection for root weight should have little effect on these.

The randomly intermating procedure used to develop material for this study necessitated a selection for increased flowering. Thus correlations with buds per cyme, the only measure of flowering included in this study, are of special interest. The positive genetic correlation with vine diameter (Table 3) is of questionable practical importance. Possible important r_G estimates occurred with root veining, root cracking and purple leaf whorls, none of which could be considered undesirable (Table 2). A few significant r_G estimates are found in Table 4, but it is difficult to assign much importance to these, since in every case one of the 2 estimates was non-significant. Most significant, perhaps, is the lack of economically important genotypic correlations with this measure of flowering.

Many of the traits studied are of little or no known economic value and as such may be considered as secondary characters. Most of the vine traits were included because of the ease with which they could be measured, and to determine if interesting relationships exist with those root traits of primary economic importance. There were some indications that increasing vine purpling was related to increased wilt susceptibility, increased root flesh oxidation and white flesh types (Table 2). Internode length and vine diameter may be related in some way to root shape. However, since the most desirable root shape was represented by intermediate scores, correlations with it are difficult to evaluate. The most interesting secondary trait was leaf vein purpling. Important genotypic correlations were found between it and root weight, and number of edible roots (Table 3). Thus, leaf vein purpling may be of value in selection for yield. A possible adverse r_G was found with it and root veining (Table 4).

Explanation of the different estimates of r_G for the 21 pairs of traits listed in Table 4 requires consideration of several factors. Since there were 420 pairs of r_G estimates tested for differences at the .01 probability level, one would expect about 4 to be different by chance. Twenty-one differences were found, certainly more than expected by chance alone. Although this study assumed randomness throughout, it recognized that certain selection was necessary. Parent plants had to flower and set enough seed to provide 15 offspring; and roots had to sprout in order to be included in second year tests. Selection was avoided and all seedlings were set in the field regardless of their vigor. Some died and had to be replanted; this compounded the effects of low vigor, since not only were such plants less vigorous than other plants in the test but they were planted later. Therefore, differences in plant vigor may explain some of the paradoxes of Table 4. Most of the character pairs in Table 4 involve at least one character which exhibited a large genotype by environment interaction such as root weight, number edible roots, root growth cracks, root veining (5), or buds per cyme (4). In the case of buds per cyme, there was selection in the parents but not in the offspring. Correlations at the high end of a distribution may well be different from those taken over all types. Thus, the differences in the cross-covariances could have been due to differences in the distribution of one or both traits in parent and offspring arrays.

Interpretations of data presented in Table 4 must be made with some reservation. However, the data suggest that selection for wilt resistance is not likely to have any affect on root veining in the next generation, but that selection for lack of root veining may be expected to result in increased wilt resistance in the ensuing generation. Certainly no adverse association is indicated. Selection for wilt resistance may reduce the number of buds per cyme in progeny of selected plants over that of the unselected population, but selection for high number of buds per cyme should have no affect on wilt resistance in the next generation. Although selection for high root weight should result in clones with wide distribution of skin colors, selection for darker skin types should provide a higher average root weight in the next generation. Selection for high root weight should result in plants with various vine lengths, but selection for long vines should increase average root weight. This may be where vigor exerts an influence; and perhaps elimination of the non-vigorous plants would eliminate this correlation. The other correlations listed may be interpreted in like manner.

Lack of previous quantitative genetic reports for sweetpotatoes make it difficult to find other results for comparison. Li (6) used path coefficient techniques to study various yield components of sweetpotato. His estimates of r_p (.76), r_G (.73) and r_E (.83) for root weight and number of roots compares favorably with my respective estimates: .88, .89 and .88. Simple correlations from one environment were determined for cycles 1 and 3 of this population in a preliminary study of variability (2). In that study the possibilities of genetic relationships were discussed for several traits; and it appeared that a r_p between leaf vein and root skin purpling should disappear in later cycles since it was related to flowering in some way. This correlation was of no importance in cycles 4 and 5. A postulated genetic linkage of root flesh oxidation and root flesh color tends to be supported by the present study. In both tests those traits with obvious physiological relationships tended to have similar phenotypic correlations in terms of direction (positive or negative), although magnitudes differed considerably. Such differences are probably due to genotype by environment interactions and environmental correlations, since the preliminary study was grown in only one environment and the present study was grown in 6 environments. The interesting association of leaf vein purpling with root weight and number of edible roots was not detected in the preliminary study.

Genetic associations predicted by parent and offspring mean differences (4) were verified by this part of the analyses. A 9% decrease in number of buds per cyme from parent to offspring indicated selection for increased numbers of buds in the parents. The concomitant 9% decrease in leaf whorl purpling in offspring would suggest a negative correlation of some kind between these 2 traits; selection for high numbers of buds in the parents would decrease leaf whorl purpling in the next generation. The r_p, r_G and r_E estimates were negative and significant (Table 2). Vine diameter was 8% larger in the offspring, a factor suggesting a positive association with buds per cyme (selection for high number of buds would produce increased vine diameters in the following generation). The r_G estimate was positive and significant (Table 3). As expected, leaf whorl purpling and vine diameter had a negative r_G (Table 3). Vine length, internode length and leaf length, the 3 traits mentioned as differing in offspring from the parents by about 5%, were not directly associated to buds per cyme, but apparently they were affected indirectly through genotypic correlation with vine diameter. There was a similar mean difference between parent and offspring generations in only one of the root traits, growth cracking. Reduction in cracking was almost 8% in the offspring (5). Thus the negative genetic correlation between number buds per cyme and growth cracking was as expected (Table 2).

No serious impediment to selection for improved horticultural types through mass selection techniques was detected. A number of genotypic correlations found suggested that selection indices may be profitable in sweet potato improvement programs.

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Breeding Behavior of Mite-Resistant Strawberries[1]

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Abstract. Backcrosses and outcrosses of mite resistant strawberry selections and combinations of resistant selfed lines were made. Backcrosses to the resistant parents resulted in intermediate progeny means but they were closer to that of the less resistant parent. Backcrosses to the susceptible parent also resulted in intermediate progeny means but they were close to that of the more resistant parent. Outcrosses gave progenies similar to those of backcrosses but with less spread in resistance. Crosses of certain resistant selfed selections showed almost complete dominance for mite resistance.

A previous publication (1) indicated that resistance to the two-spotted mite, *Tetranychus urticae,* Koch,[4] was partially dominant and controlled by multiple genes. The same study showed that selfing resulted in a loss of resistance. It was speculated that this might be due to non-additive gene action and/or a loss of vigor. It was shown that breeding for mite resistance is feasible.

This experiment was conducted to study further the breeding behavior of mite-resistant strawberries by means of backcrosses, sib crosses, outcrosses, and combinations of selfed lines.

Materials and Methods

Mite-resistant selections from crosses between resistant selections and a susceptible cultivar, 'Dixieland,' were used in this study. Table 1 shows the crosses made. Hereafter, the selections will be referred to using only their last number, as: Ky 9 instead of Ky 22-61-9. The seed from the crosses were planted when mature on ground sphagnum moss. The resulting seedlings were planted in 4″ clay pots in June and grown in the greenhouse during the remainder of the summer and fall. Parent plants were set in 4″ clay pots in August. The seedlings from each cross and plants of the parental cultivars were divided into five replications and randomized on greenhouse benches. They were inoculated with mites on October 25 as described by Chaplin et al. (1). The mites reproduced rapidly and mite injury to the plants was rated on November 7. The rating system previously described (1) by which the plants were rated

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[4] All references to mites will be to *Tetranychus urticae.*

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