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Heritabilities and Correlations in Muskmelon from Parent-offspring Regression Analyses[1]

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Abstract. **Data from 14 traits in muskmelon (*Cucumis melo* L.) were analysed by parent-offspring regression to produce estimates of heritability and phenotypic, genotypic, and environmental correlations. Heritability estimates determined from correlation coefficients ($h^2 = r$), equivalent to regression analysis on data coded in standard deviation units ($h^2 = b'$), were low (5–13%) for maturity and yield traits, and moderate (53–71%) for fruit appearance and quality traits. Soluble solids content at $h^2 = 16\%$ was the exception. Heritabilities calculated by intraclass correlations of half-sib progenies ($h^2 = 4t_{hs}$) provided many values which exceeded 100%. Phenotypic, genotypic and environmental correlations among paired traits indicated many significant and desirable relationships which could be used to reduce numbers of observations on breeding materials as well as provide guidance for selection within future muskmelon populations. Correlated responses were predicted for all traits from single-trait selection of several fruit quality characters. Predicted and realized responses in the offspring generation by simulated direct selection (10%) for each character within the parent population are presented. Priorities for trait selection and choice of breeding procedures for improvement in muskmelon are discussed. External fruit characters such as net appearance and nonindented vein tracts, or intermediate fruit size, each of which can be scored visually and rapidly, appear most suited for selection within these populations.**

Quality of muskmelon fruits produced in the southwestern states is determined by several external and internal features. Davis et al. (5) considered 14 fruit quality ratings within the cultivar 'PMR 45' grown at various locations in California. Andrus and Bohn (1) included 18 separate fruit observations in their rating system for evaluating progress in a mass selection program. Most of these characters measured quality based on visual appearance of the fruit. No data were provided on plant yields or time to fruit maturity.

Composite rating systems and selection indices have been devised to evaluate muskmelon cultivars and breeding entries based on multiple trait evaluations (1, 3). Such systems become complicated when many characters are included. Correlations previously reported for muskmelon traits relate primarily to phenotypic associations within or among commercial cultivars (5, 6, 9, 12, 14). Bohn and Andrus (2) concluded that high environmental correlations occur among certain fruit characteristics in muskmelon, but are low among others.

Knowledge of phenotypic and genotypic correlations among paired traits, or for a single trait among different generations, provides the opportunity to predict response in one trait when selection is practiced on another. Genetic correlations for traits observed in segregating populations would be useful in identifying the magnitude of variation responsive to selection, for predicting genetic advance, and for selecting a breeding scheme to best utilize this variation. Lippert and Legg (10, 11) determined by diallel analyses of 45 F_1 hybrids from crosses of 10 muskmelon cultivars that the additive component of genetic variation was important in various yield, maturity, and fruit traits in this crop.

Finally, favorable phenotypic and genotypic correlations should permit the breeder to reduce the total number of observations required on breeding materials, without adversely restricting genetic advance or altering the goals of the program.

This parent-offspring study was conducted to estimate heritabilities for important traits in muskmelon, and to measure phenotypic, genotypic and environmental correlations among these traits. Responses observed in the offspring generation from direct trait selection in parents and predicted from correlated responses calculated from these correlations and heritabilities are presented.

Materials and Methods

A population of muskmelon undergoing recurrent selection formed the basis of this parent-offspring study. The initial population had been constituted by equally intermating the 6 F_1 hybrids resulting from biparental crosses of 4 cultivars: 'Campo', 'Hale's Best 36', 'Sulfur Resistant (SR) 91', and 'Schoon's Hardshell'. A base population of 500 plants was subjected to 1 cycle of selection during 1971 (selection intensity of 10%, k = 1.76). Six plants from open-pollinated seeds of each selection were random mated the next season using pollen pooled from plants of all selected lines. Five seeds from each female plant within the random mating block provided the 500 plant population for the second selection cycle in 1973. Eighty plants from this 1973 population were chosen at random to constitute the parent generation for this study, with their open-pollinated seed forming the offspring generation in 1974. Offspring were grown in a randomized complete block design with two replications. Three plants per plot represented a given parental line.

For each generation, seeds were germinated in the greenhouse and the resulting plants transplanted to the field after 21 days. Culture was similar to commercial winter-spring muskmelon culture practiced in the Imperial Valley, with the exception of a 2.13 m^2 plant spacing to provide records on individual plants.

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Fruits judged mature by the formation of an abscission zone (half-slip or greater) were harvested at 2- to 3-day intervals over a 4-week period in May and June. Data on 14 traits, including maturity, yield, and other fruit characteristics, were obtained on individual plants and fruits (Table 1). Vein tracts, the longitudinal indentations or unnetted stripes (4), and net, the network of suberized cork cells (15) on the fruit surface, were each scored subjectively on a scale of 1 to 5, with 5 representing indistinguishable vein tracts, or dense netting over the entire fruit surface. Percentage flesh was calculated from measurements of the fruit diameter as: % flesh = [width — cavity diameter — 2(rind thickness)] 100/ width.

Regression coefficients, b, were calculated for each trait from female parent values and offspring means. Heritability was estimated from regression coefficients as $h^2 = b$, consistent with parent-offspring studies (13). This equation assumes S_1 progeny from random mated parents. Even though muskmelons are predominantly insect pollinated, the andromonoecious flowering pattern, coupled with the wide plant spacing in this study, is assumed to favor selfing in a high percentage of the pollinations of parent plants.

Heritabilities were also calculated for each trait from correlation coefficients on original data, $h^2 = r$, which is equivalent to the standard unit heritability, $h^2 b'$, of Frey and Horner (8). These estimates cancel any scaling effects based upon environmental factors which may influence phenotypic variability due to culture of parents and offspring in different seasons (8). Finally, heritabilities were estimated as intraclass correlations among half-sib progenies, $h^2 = 4t_{hs}$ (7).

Phenotypic correlations (r_p) for paired traits were calculated directly from parent measurements. Genotypic correlations (r_G) were computed (7) as $r_G = cov_{xy} / \sqrt{cov_{xx} \cdot cov_{yy}}$, where cov_{xy} is the 'cross covariance' (parental value for trait x times the mean offspring value for trait Y) and cov_{xx} and cov_{yy} are the respective parent-offspring covariances for each trait. The cross covariance was computed in 2 ways (X trait in parent by Y trait in offspring and vice versa) giving 2 estimates of r_G. Where these two estimates were not different at the 1% probability level, they were averaged.

The environmental correlation (r_E) for paired traits was estimated by the equation (7): $r_p = h_x h_y r_G + e_x e_y e_E$, where r_p is the phenotypic correlation, h_x and h_y are square roots of heritabilities for traits x and Y, and e_x or e_y are equal to $\sqrt{1 - h^2}_{x \text{ or } y}$.

Correlated responses were predicted from Falconer's (7) equation: $CR_Y = k\, h_x\, h_y\, r_G\, \sigma_{PY}$, where CR_y, the response in trait Y when selection was applied to trait X, equals the product of k, the selection intensity imposed on the parent population, h_x, h_y, the square roots of heritabilities for traits X and Y, r_G, the genetic correlation of X in parents, Y in offspring, and σ_{PY}, the phenotypic standard deviation of Y in parents. A single selection intensity of 10% ($k = 1.76$) was evaluated. Responses predicted in offspring from these CR_Y values were expressed as a percentage of the overall parent means $(CR_Y)(100) / P$.

Values predicted for a trait by direct selction were calculated as $(\bar{P}_S - \bar{P})(100) / \bar{P}$, with $\bar{P}_S$ the mean of selected parents and $\bar{P}$ the overall parent mean. Realized changes by direct selection were estimated as a percentage change in the offspring generation from the formula $(\bar{O}_S - \bar{O})(100) / \bar{O}$, where $\bar{O}_S$ represents the mean of offspring from selected parents and $\bar{O}$ the overall offspring mean for the selected trait.

Results and Discussion

Mean performance for the 14 measured traits in parent and offspring generations are presented in Table 1. In general, plants in the offspring generation required more days from transplanting to first matured fruit. However, the period between first and third fruit harvested, and the duration of the harvest period were shorter for the offspring generation. Also, average weight of fruit and fruit length and width were greater from offspring plants. In features related to fruit quality, the trend was for lower averages among offspring compared to parents. These mean values involve differences in environmental conditions due to production season as well as genetic differences due to generations.

The 3 methods used to calculate heritability provided different estimates (Table 1). Many values determined from intraclass correlations of half-sib families greatly exceeded 100%, while estimates based on uncoded regression coefficients ($h^2 = b$) were consistently lower than those from correlation coefficients ($h^2 = r$). Heritability estimates based on correlations coefficients correct for phenotypic variability between generations grown in different seasons, which may be due to genotype-environment interactions. Also, these correlatons from parent-offspring data establish a ceiling of 100% for heritability estimates (8). Therefore, values of $h^2 = r$ were considered as estimates of heritability for these traits, and were used in calculations for environmental correlations.

Heritability estimates were low (5–13%) for days from transplant to various fruit maturities, and for numbers and total weights of fruit havested. Fruit set and fruit development on muskmelon plants are greatly influenced by the environment, and genetic control of these characteristics could be expectd to be low. Heritabilities for fruit appearance and quality traits were relatively high (53-71%) with the exception of percent soluble solids (16%).

Phenotypic (r_P), genotypic (r_G) and environmental (r_E) correlations for paired traits are presented in Table 2 and 3. Table 2

Table 1. Means of parent and offspring generations and heritability estimates for 14 muskmelon traits.

Traits	Means		Heritability^z (h^2)		
	Parents	Offspring	b	4ths	r
Individual plants:					
Days, transplant to first fruit harvested	91.5 ± 5.3	108.9 ± 3.6	.07	.80	.11
Days, 1st to 3rd fruit harvested	10.1 ± 6.4	9.3 ± 3.2	.06	.22	.13
Days, 1st to last fruit harvested	17.6 ± 6.9	12.3 ± 3.4	.03	.35	.05
No. of fruit harvested per plant	5.8 ± 1.7	4.8 ± 1.2	.07	–.09	.12
Total wt of fruit harvested (g)	6508 ± 1909	6473 ± 1432	.06	–.05	.09
Individual fruits:					
Avg wt of fruit harvested	1151 ± 219	1350 ± 196	.47	.77	.52***
Net appearance^y	4.0 ± 0.7	3.7 ± 0.5	.47	1.61	.65***
Vein tracts^y	3.3 ± 0.6	3.0 ± 0.4	.39	1.04	.56***
Soluble solids (%)	12.4 ± 1.2	11.5 ± 0.8	.10	.42	.16
Flesh (%)	48.0 ± 3.9	45.8 ± 3.4	.60	1.59	.71***
Rind thickness (mm)	4.4 ± 1.6	4.7 ± 1.4	.65	1.93	.71***
Length (mm)	146.0 ± 12.9	152.9 ± 10.2	.49	.82	.61***
Width (mm)	136.1 ± 10.0	141.2 ± 8.0	.44	.85	.55***
Shape index (L/W)	1.07 ± .07	1.08 ± .05	.45	1.28	.60***

[z] b is the regression coefficient, ths is the intraclass correlation among half-sib progenies, and r is the correlation coefficient among parental values.

[y] Subjective scale of 1–5, with 5 indicating heavily netted fruits, or indistinguishable vein tracts.

***Significant at the 0.1% level.

Table 2. Correlations for pairs of traits for which rG estimates were different at 1% probability, and for which 2 estimates of rE were computed.

Traits		Correlations^{z}				
			Genotypic (rG)		Environmental (rE)	
x	y	Phenotypic (rp)	xy	yx	xy	yx
Days to 1st fruit	Days, 1st to 3rd fruit	–.58***	–1.29	–.34**	–.49***	–.62***
	Days, 1st to last fruit	–.61***	–.92***	1.92***	–.58***	–.82***
	No. fruit harv.	–.02	1.29	.99	–.15	–.15
	Length	.25**	.85***	.20	.05	.34**
	Width	.11	.76***	.34**	–.12	.04
	% sol. solids	–.31**	1.53	1.44	–.60***	–.58***
	Shape index	.21	.41***	–.13	.17	.40***
Days, 1st to 3rd fruit	Days, 1st to last fruit	.56***	1.04	.85***	.52***	.53***
	No. fruit harv.	–.05	–.79***	.06	.05	–.07
	Total weight	.02	–1.11	.37***	.16	–.02
	% sol. solids	.37***	–2.03	.12	.78***	.42***
	Rind	.16	.73***	–.11	.11	.40***
Days, 1st to last fruit	No. fruit harv.	.33**	–1.42	–.13	.49***	.37**
	Total wt	.24*	–3.25	–.82***	.48***	.31**
	Length	–.17	–.58***	–.12	–.12	–.25*
	Width	.00	–.84***	–.31**	.22*	.08
	Net	–.04	–.83***	–.39***	.20	.06
	Vein tract	–.13	–1.33	–.40***	.15	–.10
	Rind	.27*	.36**	–.15	.40***	.57***
No. fruit harv.	Wt/fruit	–.33**	–1.04	–.55***	–.25*	–.31*
	Width	–.26*	–1.24	–.53***	–.11	–.19
	Shape index	.05	.58***	.03	–.17	.08
	Rind	.02	.37***	–.06	–.18	.08
Total wt	Length	.39***	.96***	.89***	.28*	.31**
	Width	.35**	.58***	.83***	.36**	.27*
	Vein tract	.09	.86***	–.84***	–.15	.44***
	Shape index	.13	.68***	.32**	.04	.09
	Flesh %	.26*	.25*	.65***	.39***	.19
	Rind	.04	.79***	–.02	–.30**	–.09
Length	% sol. solids	–.20	–.25	–.69***	–.21	–.04
% sol. solids	Net	.09	.07	–.41***	.13	.41***
	Vein tract	–.07	–.49***	.11	–.14	–.18
	Shape index	–.44***	–.67***	.15	–.40***	–.84***

^{z}The first trait indicated x or y was from parent generation, with second trait (y or x) from offspring as explained in text for calculations of cross-covariances.

*,**,***; significant correlations at 5% (*), 1% (**), and 0.1% (***) levels.

contains those comparisons for which the two estimates of r_G were significantly different at the 1% probability level, or were greater than 1 or -1. Table 3 consists of comparisons in which the two estimates of r_G were averaged, and a single r_E computed. Only those pairs of traits with significant r_P or r_G estimates are included in these tables.

In each of the paired comparisons in Table 2, the heritability estimate was low for one or both traits. In those comparisons where r_P was significant, r_E values were of the same sign as the r_P and generally of equivalent magnitude. Phenotypic correlations, therefore, may be due chiefly to the environmental correlations (7). Interpretation of these data (Table 2) and application to a melon breeding program must be made with some reservation. However, the data suggest that selection for early fruit maturity might result in an increased maturity period for additional fruits on these vines. Selection for concentrated harvest, to the contrary, might lead to earlier maturity of fruits. Within the fruit quality traits, selection for high soluble solids may reduce fruit length and shape index, and increase vein tract expression, without affecting net appearance. Selection for either fruit length or net might decrease soluble solids, whereas selection for vein tracts or shape index should not affect soluble solids in the next generation. Other comparisons in the table may be similarly interpreted.

The phenotypic, genotypic, and environmental correlations for paired traits in Table 3 suggest several associations of importance to the muskmelon breeder. In several comparisons, the r_E reinforced the r_G, and the r_P was significant. Net appearance and vein tracts provided positive values for each type of correlation, while net appearance and shape index or rind thickness produced negative values. Selection for high net expression should result in fruit with indistinguishable vein tracts, thinner rinds, and more nearly rounded shapes in the next generation due both to genetic and environmental causes.

Other associations involved pairs of traits with nonsignificant r_P, but which were correlated genotypically, sometimes with an r_E of opposite sign. As examples, percent soluble solids and average fruit weight, fruit width or rind thickness had significant negative r_G which were offset by positive r_E, such that r_P values

Table 3. Correlations of pairs of traits for which estimates of rG were averaged and rE were computed.

Traits		Correlations		
		Phenotypic (rp)	Genotypic (rG)	Environmental (rE)
Days to 1st fruit	Wt/fruit	.19	.60***	.07
	Vein tract	.04	.28*	–.05
	Flesh %	.10	–.28*	.34**
Days, 1st to 3rd fruit	Vein tract	–.12	–.30**	–.07
	Shape index	–.18	–.29**	–.16
Days, 1st to last fruit	Wt/fruit	–.13	–.65***	–.03
	% sol. solids	.44***	–.01	.50***
	Shape index	–.23*	.09	–.35**
	Flesh %	–.09	.51***	–.35**
No. fruit harvested	Total wt	.75***	–.32**	.88***
	Length	–.18	–.48***	–.19
	% sol. solids	–.05	.38***	–.12
	Net	–.09	–.34**	–.02
	Flesh %	.19	.43***	.13
Wt/fruit	Total wt	.35**	.86***	.25
	Length	.83***	.87***	.79***
	Width	.92***	.96***	.87***
	% sol solids	.02	–.59***	.30*
	Net	.27*	.14	.47***
	Vein tract	–.14	–.32**	.08
Total wt	% sol. solids	–.06	–.48***	–.10
Length	Width	.73***	.74***	.72***
	Shape index	.55***	.61***	.47***
	Rind	.16	.27*	.07
Width	% sol. solids	.12	–.40***	.39***
	Net	.39***	.32**	.50***
	Vein tract	–.16	–.34**	–.07
% soluble solids	Rind	.07	–.41***	.42***
Net	Vein tract	.60***	.44***	.86***
	Shape index	–.45***	–.43***	–.47***
	Rind	–.37***	–.34**	–.44***
Vein tract	Flesh %	.26*	.36**	.10
	Rind	–.52***	–.49***	–.62***
Shape index	Rind	.22*	.29**	.11
Flesh %	Rind	–.60***	–.61***	–.56***

*,**,*** are significant correlations at 5% (*), 1% (**), and 0.1% (***) levels.

were negligible. These correlations suggest that plants which produced fruits with high soluble solids due to genetic influences tended to produce lighter, narrower fruits with thin rinds. Conversely, plants producing fruits with high soluble solids due to environmental causes tended toward heavier, wider fruits with thicker rinds. The genotypic and environmental causes of variation may affect these traits through different physiological mechanisms (7). Environmental sources of variation, therefore, tended to offset the desired genotypic effects among these traits.

Other comparisons provided significant r_P among traits without evidence of genetic correlations, such as days from first to last fruit harvested and shape index, or average fruit weight and net appearance. In each instance, low heritability was estimated for the first trait of each pair, so that the significant r_P could be accounted for by the large r_E. Selection for either trait within these paired comparisons should have little effect on expression of the other trait.

Correlated responses in all traits (y) based on selection for the fruit measurement and quality traits (x) calculated from the correlations and heritability estimates are presented in Table 4. Tabular values represent changes predicted in the next generation as a percentage of the parent means. The presentation in the table is limited to selection on those traits which provided significant h^2 estimates and/or were most easily measured.

From an examination of these predicted responses, it appears that selection for maximum net appearance, reduced vein tract expression or reduced rind thickness would offer favorable responses in other, nonselected traits. Selection for each of these three traits predict desirable changes (9–19%) in the other two, without serious, adverse effect on other traits. Verification of these predictions can only be obtained by actual selection and testing.

Simulated direct selection of the superior 10% of the parent population was evaluated in the offspring generation (Table 5). Realized change was in the direction as predicted, with the exception of the fruit maturity traits, whereas magnitude of the realized change was consistently below the predicted level. These data do provide important information to the breeder on types and extent of progress to be expected from direct selection for individual traits.

Table 4. Correlated responses predicted for traits y based upon selection for traits x at 10% selection intensity. Values are expressed as percentage change predicted in offspring.

	Percentage change							
	Selected traits (x)							
Correlated trait (y)	Net	Vein tract	Avg fruit wt (small)	No. fruit	% soluble solids	Rind^z thickness	Flesh %	Shape^z index
No. fruit harvested	–5	–2	7	—	3	1	6	0
Total fruit wt	–2	–10	–9	–2	–3	0	8	–4
Avg fruit wt	3	–6	—	–9	–6	–2	0	–3
Vein tract	12	—	8	16	–7	14	10	–2
% soluble solids	–2	1	3	1	—	2	0	–1
Flesh %	–1	3	0	2	0	6	—	–2
Rind thickness	–15	– 19	–3	7	–9	—	–28	–12
Length	0	–2	–8	–2	–3	–3	0	–6
Width	2	–2	–7	–4	–2	–1	–2	1
Shape index (L/W)	–3	0	– 1	2	–2	–2	1	—
Net appearance	—	10	–3	–4	1	9	–3	11

^{z}Selection for thin rind and shape index (L/W) = 1.0.

Table 5. Response to direct selection for each muskmelon trait as predicted from 10% parental selection and realized in the offspring generation produced from these selections.

Trait	Percentage change	
	Predicted	Realized
Days, 1st fruit harvested	–6	0
Days, 1st–3rd fruit	–95	19
Days, 1st–last fruit	–74	0
No. fruit harvested	50	4
Total fruit wt	45	11
Avg. fruit wt (largest)	33	12
Avg. fruit wt (smallest)	–31	–20
Net appearance	29	17
Vein tract	36	12
Soluble solids (%)	13	4
Flesh (%)	14	9
Rind thickness	–50	–30
Length (longest)	15	5
Length (shortest)	–16	–10
Width (widest)	13	4
Width (narrowest)	–13	–10
Shape index (L/W)	–11	–7

Conclusions

The correlations among traits developed from this parent-offspring study provide valuable information for reducing the number of traits to be evaluated in muskmelon breeding programs. The external fruit characters of net and vein tract expression were easily observed and rated, and provided several significant phenotypic and genotypic correlations with other, less readily measured, traits. The subjective, nonparametric measure for net and vein tract, followed by parametric analyses of these data imposes a source of error for these estimates. Therefore, the correlations and correlated responses involving these traits must be verified by additional experimentation. Fixation of dense net coverage and nondistinguishable vein tracts should be possible, since commercial cultivars such as 'Topmark' and 'Topscore' possess this phenotype.

Vein tracts as a selection criterion produced the best predicted correlated responses. The melon breeder could select within a variable population for this visual trait until the desired expression for vein tract was accomplished, then select, successively, for other traits. Such tandem selection would require considerable time where may characters were involved. There would also be the possibility for loss of valuable genetic variability associated with other traits during selection for a single trait.

Concurrent selection for several traits would offer more rapid improvement, although maximum expression in some or all traits may be sacrificed. Selection could be based upon independent culling levels, with advancement to the next generation only of those individuals which met an established minimum value for each trait, or could be based on genetic and economic merit associated with each trait, as in index selection.

Intercrossing among selections to establish the next population for selection, as in simple recurrent selection, should provide opportunity to increase the frequency of desirable genes in the population and thus increase expression of traits in advanced generations. Recombinations through intercrossing could effect linkage relationships and alter genetic correlations among traits.

The correlated responses predicted from this muskmelon population suggest that selection for a few characters mights provide concurrent improvement in the many characters related to muskmelon quality. Fruits could be scored rapidly for several visual traits throughout the harvest period. Priorities for selection could be the minimal expression of vein tracts on intermediate sized, round fruits with maximum surface netting.

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