

Inheritance of fruit yield in two watermelon populations in North Carolina

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Abstract Elite cultivars of watermelon (*Citrullus lanatus* (Thunb.) Matsum. & Nakai) are high in fruit quality but may not be the highest yielders. The objective of this study was to estimate the heritability of, and genotypic and phenotypic correlations among, yield traits in two watermelon populations developed from crosses between obsolete cultivars with high yield and elite modern cultivars. Field trials were conducted at two locations in North Carolina (Clinton and Kinston). The data were analyzed by regressing $S_{0:1}$ progeny data on S_0 parent data to estimate narrow-sense heritability. Narrow-sense heritability estimates were low for all traits measured [total fruit weight (0.04–0.12), marketable fruit weight (0.06–0.15), total fruit number (0.04–0.16), fruit size (0.18–0.19), and percent culls (0.02–0.09) in North Carolina Watermelon 1 (NCWP1) and North Carolina Watermelon 2 (NCWP2) populations, respectively]. Estimates of broad-sense heritability were higher than estimates of narrow-sense heritability. Total fruit weight and marketable fruit weight were highly correlated ($r_g = 0.97$ – 1.00). Marketable fruit weight and fruit size used as single selection criteria

in NCWP1 and total fruit number in NCWP2, were predicted to give the best correlated response for total fruit weight. Narrow-sense heritability was low for fruit yield; therefore, watermelon breeders should select based on replicated progeny rows in multiple environments to maximize gain.

Keywords *Citrullus lanatus* · Narrow-sense heritability · Parent-offspring regression
Predicted gain · Correlated response

Abbreviations

Mark	Marketable
Wt.	Weight
No.	Number
TSS	Total soluble solids

Introduction

High yield is a major objective in many crop breeding programs. In the last decade, yield increases in watermelon have been attributed to improved production techniques as well as to the use of cultivars resistant to biotic and abiotic stresses (Maynard 2001). In the USA, the better growers may get 51 Mg ha^{-1} of marketable fruit (Maynard 2001), but the average yield of watermelon in 2008 was 32 Mg ha^{-1} . Plant breeders have spent considerable effort to improve quality traits (TSS, flesh color, and fruit shape). Previous innovations in watermelon

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breeding include uniform inbreds and hybrids, seedless triploid hybrids, and mini sized watermelons. Although most cultivars have high quality and uniformity, higher yield would be of interest to growers. Gusmini and Wehner (2005) reported large differences in yield among a diverse array of elite and obsolete watermelon cultivars tested in three environments in North Carolina. Some of the obsolete cultivars had high yield, and it would be useful to transfer that to elite cultivars such as the hybrid 'Sangria', a leading cultivar in the Southeastern USA for the last decade in the seeded watermelon market.

Watermelon breeders usually produce hybrid cultivars because of the ease of protecting intellectual property rights of the parental lines, as well as the small amount of heterosis for yield (Gusmini and Wehner 2005). Watermelon researchers have reported heterosis in studies of general and specific combining ability (Bansal et al. 2002a, b; Brar and Sidhu 1977; Brar and Sukhija 1977; Gopal et al. 1996). Hybrids are also required for the production of seedless cultivars using triploids (Maynard 2001).

Complex traits, such as yield, are often controlled by multiple genes or quantitative trait loci (QTL). In order to develop an efficient breeding program, estimates of heritability and number of effective factors (genes) are required, as well as knowledge of the mode of gene action. Broad-sense heritability for yield has been estimated for watermelon (Gill and Kumar 1986; Prasad et al. 1988; Vashistha et al. 1983). However, narrow-sense heritability estimates would be more useful for inbred line development, since they exclude the estimates of non-additive variance that is not fixable. Heritability can be expressed based on single plants, progeny, or progeny row means (Holland et al. 2003; Nyquist 1991). Heritability estimates can be used to make decisions about the most effective methods to use in plant breeding. If narrow-sense heritability for watermelon yield were high, yield of elite inbreds could be improved by backcrossing them to high yielding lines. However, if yield has low narrow-sense heritability, recurrent selection or other long-term breeding approaches will be needed to develop high yielding lines. Recurrent selection in diverse populations has been used in cross-pollinated crops, such as maize, to improve the germplasm base (Lamkey 1992; Weyhrich et al. 1998).

The relationship between parent and offspring is of specific interest in breeding programs where direct

resemblance is useful in programs using mass selection or selection indices (Baker 1986; Lynch and Walsh 1998). Parent-offspring regression also is a useful method for obtaining estimates of narrow-sense heritability.

The objectives of this study were to estimate narrow-sense heritability for yield in two watermelon populations, and to measure genotypic and phenotypic correlations among several yield traits.

Materials and methods

Germplasm and crosses

In this experiment, we developed two watermelon populations, North Carolina Watermelon Population 1 (NCWP1) and North Carolina Watermelon Population 2 (NCWP2) using a diverse set of cultivars. High yielding obsolete cultivars with poor quality fruit were chosen, along with elite cultivars having good flesh color, high total soluble solids (TSS), and disease resistance. Cultivars were divided into two sets, with six cultivars in each set. Cultivars in each set were crossed to generate a half-diallel. Set 1 consisted of Calhoun Gray, Dixielee, Mountain Hoosier, Big Crimson, Starbrite, and Legacy. Set 2 had Red-N-Sweet, Big Crimson, Sangria, Early Arizona, Charleston Gray, and Star-N-Stripes. High-yielding cultivars were crossed with elite cultivars to develop F_1 . To develop NCWP1, F_1 individuals were self- and sib-pollinated in the greenhouse to obtain S_0 seeds to use as the starting cycle for the NCWP1 population. To develop NCWP2, F_1 individuals were planted in field as single-plant hills, and were allowed to open-pollinate to obtain S_0 seeds to use as the starting cycle for the NCWP2 population.

Cultural practices

The experiment was conducted at the Horticultural Crops Research Station, in Clinton, NC, and at the Cunningham Research Station, in Kinston, NC. Cultural practices were based on recommendations by the North Carolina Extension Service (Sanders 2004). The soil type at Clinton was Orangeburg loamy sand (fine-loamy, kaolinitic, thermic Type, Kandiuults), and that at Kinston was Norfolk sandy loam (fine-loamy, kaolinitic, thermic Typic Kandiuults). Soil

was fumigated with Telone C-17 (1,3-Dichloropene + Chloropicrin) applied at a rate of 27 kg ha⁻¹. Fertilizer was incorporated before planting at a rate of 90–39–74 kg ha⁻¹ (N–P–K) with an additional 34 kg ha⁻¹ at tip-over stage. Irrigation was applied for a total (including rainfall) of 25 to 40 mm per week.

Each parent plant was manually trained each week in a spiral by turning all the vines in a clockwise circle around the crown until fruit-set began (Gusmini and Wehner 2007). Plant training allowed accurate identification of each fruit and plot. No disease problems were observed. Fruit were harvested when more than 90% were ripe. Fruit were determined to be ripe using several indices: a dried tendril nearest the fruit, a light colored ground spot, dull not shiny rind, and a dull not metallic sound of the melon when thumped (Maynard 2001).

Parental and progeny evaluation

A large number of S₀ parents (320) were grown as single plant hills in the summer of 2006 for NCWP1 and 2007 for NCWP2 at Clinton. The fields had raised beds on 3.1 m centers, and S₀ plants were spaced 3.05 m apart. Seeds were extracted from one fruit from each parent plant to be used as offspring (S_{0:1} progenies) in the following year. S_{0:1} seeds were the result of self-pollination (Kumar 2009). The 240 S_{0:1} progenies with sufficient seeds for progeny testing were selected at random to be planted in summer of 2007 for NCWP1 and 2008 for NCWP2 populations at two locations, Clinton and Kinston. S_{0:1} progeny were planted with six plants per plot. Plots were 3.7 m long, with 0.6 m between hills, and 2.5 m alleys at the end of each plot.

Heritability was determined for total fruit yield (Mg ha⁻¹), marketable fruit yield (Mg ha⁻¹), total fruit number per hectare, fruit size (kg per fruit), and percent culls (%). All bottlenecked, undersized, and deformed fruits were recorded as cull fruit.

Narrow-sense heritability

Estimates of narrow-sense heritability of yield traits in each population were made by regressing the mean S_{0:1} family values on their S₀ parental values using PROC REG procedure of SAS (2002, SAS 9.1, SAS Institute, Cary, NC) (Table 2). For this study, the

inbreeding coefficient of the S₀ population was assumed to be zero as in the case of a random-mating population. In the case of F = 0 in the S₀ generation where two equally frequent alleles exist, the single locus covariance is Cov S₀/S_{0:1} = $\sigma_A^2 + (1/2)\sigma_D^2$ (Nyquist 1991; Holland et al. 2003). This differs from the formulation given by Frey and Horner (1957), where Cov S₀/S_{0:1} was equated to $\sigma_A^2 + (1/4)\sigma_D^2$, ignoring epistasis. Smith and Kinman (1965) suggested a correction factor to account for inbreeding in such estimates, but Nyquist (1991) reported that the factor was incorrect. The regression coefficient or narrow-sense heritability is $b_{S_1:S_0} = h_n^2 = [\sigma_A^2 + (1/2)\sigma_D^2 + \sigma_{AA}^2]/\sigma_P^2$, where σ_A^2 , σ_D^2 , σ_{AA}^2 and σ_P^2 are additive, dominance, additive × additive and phenotypic variances, respectively (Holland et al. 2003). Estimates of narrow-sense heritability are biased upward because of dominance and epistatic genetic variances. The standard error of the estimated heritability was obtained by using the standard error of the estimated regression slope. The *t*-test of the slope was used (Steel et al. 1997) to test the significance of heritability. Parents and progenies were grown in separate environments to reduce the bias caused by correlation of genotype × environment interaction covariance between parent and offspring (Casler 1982). Distributions of S₀ and S_{0:1} progenies were tested for normality using Shapiro–Wilk's statistics (Shapiro and Wilk 1965) via PROC UNIVARIATE procedure of SAS-STAT.

Broad-sense heritability

Broad-sense heritability was estimated as the ratio of genotypic and phenotypic variance (Table 2). Variance components were calculated using the method of moments via PROC ANOVA procedure of SAS-STAT (2002, SAS Institute Inc. Cary, NC).

Realized heritability

There are several methods to estimate realized heritability (Nyquist 1991). In this study, it was estimated as a ratio of observed response to the selection differential (Table 2). The superior 10% of parents (S₀ individuals) were selected based on trait value. Selection differential was calculated by subtracting the mean of selected individuals in the

parental generation from the mean of overall parental populations. The difference between the performance of offspring of the selected individuals and the mean of all the progeny was used as the observed response to selection.

Genetic correlation and phenotypic correlation

In addition to heritability, the genotypic and phenotypic correlations for paired traits were also estimated using multivariate restricted maximum likelihood estimation via SAS Proc MIXED procedure of SAS-STAT (2002, SAS Institute Inc. Cary, NC) (Table 1).

Generally, ' r_g ' is defined as the correlation between genetic effects for traits X and Y (Table 1). Genetic correlation (r_g) was calculated as: $Cov G_x G_y / (\sqrt{(\sigma^2 G_x \sigma^2 G_y)})$, where, $Cov G_x G_y$ is the covariance between genetic effects of trait X and trait Y, $\sigma^2 G_x$ is genetic variance of trait X, and $\sigma^2 G_y$ is genetic variance of trait Y in $S_{0:1}$ progeny. The phenotypic correlation (r_{ph}) was calculated as: $M_{xy} / (\sqrt{M_{xx} M_{yy}})$, where M_{xy} is the mean product of trait X and trait Y, and M_{xx} and M_{yy} are the mean squares for the traits X and Y in $S_{0:1}$ progeny.

Predicted gain

The predicted gain from selection per cycle was predicted as: $h_n^2 \sqrt{\sigma_p^2}$ multiplied by the selection differential in units of standard deviations, k , for a

selection intensity of 10% ($k = 1.76$) (Hallauer and Miranda 1988) (Table 2). Realized gains from selection were also calculated by substituting narrow-sense heritability (h_n^2) using realized heritability (h_r^2) in the formula above (Table 2).

Predicted responses ($PR_{Y:X}$)

Predicted response to gain from selection per cycle was calculated using the equation: $k h_x h_y r_g \sqrt{\sigma_p^2}$ (Falconer and Mackay 1996), where $PR_{Y:X}$, the response in trait Y when selection was applied to trait X. The selection differential was k at 10% selection intensity (1.76 standard deviations); h_x and h_y were the square roots of heritability for trait X and Y, respectively; r_g was genetic correlation between trait X and Y based on $S_{0:1}$ progeny (Table 1) and $\sqrt{\sigma_p^2}$ was the phenotypic standard deviation of Y in parents (Table 3). Response to indirect selection was also calculated using parent-offspring data (Table 3). The superior 10% of individuals in the parental generation were selected for the trait, and response for indirect selection was evaluated in the offspring generation of individuals selected for other traits.

Results and discussion

The estimated phenotypic and genotypic correlations among paired traits in Table 1 suggested several

Table 1 Genotypic and phenotypic correlations (*italicized*) between paired traits for two watermelon populations

Trait	Total fruit wt.	Total fruit no.	Mark. fruit wt.	Fruit size	Percent culls
<i>Correlations for NCWP1</i>					
Total fruit wt.	–	–0.02 ^{NS}	0.97***	0.66***	–0.38
Total fruit no.	0.52***	–	0.03 ^{NS}	–0.74	–0.21
Mark. fruit wt.	0.91***	0.40***	–	0.54***	–0.60***
Fruit size	0.37***	–0.49	0.32***	–	0.14
Percent culls	–0.13**	–0.08	–0.49***	0.10	–
<i>Correlations for NCWP2</i>					
Total fruit wt.	–	0.31	1.00***	0.53*	–1.34
Total fruit no.	0.64***	–	0.40***	–0.67**	–0.77***
Mark. fruit wt.	0.97***	0.60***	–	0.44	–1.30
Fruit size	0.31***	–0.46***	0.30	–	0.23
Percent culls	–0.03	0.07***	–0.23***	0.04	–

*, **, *** Significant at $P \leq 0.05, 0.01$ or 0.001 , respectively

^{NS} Not significant at $P \leq 0.05$

Table 2 Variances, heritability estimates, and genetic gain of watermelon population NCWP1 and NCWP2

	μ^a	σ_A^2 ^b	σ_P^2 ^c	h_n^2 ^d	h_b^2 ^e	h_r^2 ^f	ΔG_P ^h	ΔG_r ⁱ
<i>NCWP1</i>								
Total fruit wt. (Mg ha ⁻¹)								
Kinston	49.53	7.61	761.28	0.01	–	0.08	0.48	3.89
Clinton	44.53	45.68	761.28	0.06	–	0.06	2.88	2.95
Overall	46.48	30.45	761.28	0.04	0.13	0.07	1.94	3.40
Total fruit no. (ha ⁻¹)								
Kinston	9.51×10^3	10^6	2.50×10^7	0.04	–	0.19	352.04	1672.20
Clinton	6.84×10^3	1.25×10^6	2.50×10^7	0.05	–	–0.08	440.05	–704.09
Overall	8.17×10^3	1.12×10^6	2.50×10^7	0.04	0.11	0.05	352.04	440.05
Mark. fruit wt. (Mg ha ⁻¹)								
Kinston	43.33	28.88	722.17	0.04	–	0.08	1.89	3.78
Clinton	40.73	65.00	722.17	0.09	–	0.05	4.26	2.36
Overall	42.03	43.33	722.17	0.06	0.15	0.07	2.84	3.31
Fruit size (kg)								
Kinston	5.90	1.17	6.17	0.19	–	–0.02	0.83	–0.09
Clinton	7.07	1.05	6.17	0.17	–	0.21	0.74	0.92
Overall	6.48	1.11	6.17	0.18	0.31	0.10	0.79	0.44
Percent culls (% by weight)								
Kinston	19.27	26.70	445.06	0.06	–	–0.48	2.23	–17.82
Clinton	13.15	–4.55	445.06	–0.01	–	0.42	–0.37	15.60
Overall	16.21	8.90	445.06	0.02	0.06	–0.03	0.74	1.11
<i>NCWP2</i>								
Total fruit wt. (Mg ha ⁻¹)								
Kinston	97.14	51.14	300.80	0.17	–	0.83	5.19	25.34
Clinton	59.07	21.06	300.80	0.07	–	–0.62	2.14	–18.92
Overall	78.11	36.01	300.80	0.12	0.21	0.12	3.66	3.66
Total fruit no. (ha ⁻¹)								
Kinston	10^4	1.93×10^6	1.01×10^7	0.19	–	0.23	1066.76	1291.35
Clinton	9.36×10^3	1.32×10^6	1.01×10^7	0.13	–	0.11	729.89	729.89
Overall	9.72×10^3	1.62×10^6	1.01×10^7	0.16	0.16	0.23	898.33	1526.14
Mark. fruit wt. (Mg ha ⁻¹)								
Kinston	94.99	53.10	279.52	0.19	–	0.86	5.59	25.31
Clinton	56.39	27.95	279.52	0.10	–	–0.64	2.94	–18.83
Overall	75.39	41.93	279.52	0.15	0.22	0.16	4.41	4.71
Fruit size (kg)								
Kinston	10.09	1.77	7.09	0.25	–	0.62	1.17	2.90
Clinton	6.76	0.92	7.09	0.13	–	–0.19	0.61	–0.89
Overall	8.43	1.35	7.09	0.19	0.32	0.21	0.89	0.98
Percent culls (% by weight)								
Kinston	4.19	9.32	310.65	0.03	–	0.30	0.93	9.31
Clinton	7.87	46.60	310.65	0.15	–	–0.16	4.65	–4.96

Table 2 continued

	μ^a	σ_A^2 ^b	σ_P^2 ^c	h_n^2 ^d	h_b^2 ^e	h_r^2 ^f	ΔG_P ^h	ΔG_r ⁱ
Overall	6.03	27.96	310.65	0.09	0.26	0.07	2.79	2.17

μ^a Population mean of parental (S_0) generation

σ_A^2 ^b Additive variance; it is overestimated by dominance and epistatic genetic variances

σ_P^2 ^c Phenotypic variance of parental ($S_{0.1}$) generation

h_n^2 ^d Narrow-sense heritability

h_b^2 ^e Broad-sense heritability

h_r^2 ^f Realized heritability

ΔG_P ^h Predicted gain from selection at 10% selection intensity ($k = 1.76$) = $k h_n^2 \sigma_P$

ΔG_r ⁱ Realized gain from selection at 10% selection intensity ($k = 1.76$) = $k h_r^2 \sigma_P$

Population size = NCWP1: 225; NCWP2:200

associations that would be useful for watermelon breeders. Total fruit weight showed high positive genotypic and phenotypic correlation with marketable fruit weight, suggesting that most of fruit weight harvested was marketable. Total fruit weight and marketable fruit weight also showed an appreciably high positive genotypic and phenotypic correlation with fruit size (weight per fruit). These results suggest that selecting for larger fruit would produce higher total and marketable yields. However, the market is oriented towards particular fruit sizes, such as micro ('New Hampshire Midget'), mini ('Petite Sweet'), small ('Sugar Baby'), medium ('Crimson Sweet'), and large ('Charleston Gray'). Thus, watermelon breeders are restricted by the market requirements from using fruit size to increase yield, but it appears that high yield would be easier to obtain using small fruit size. Total fruit weight showed a significant positive phenotypic correlation with total fruit number in both populations. However, correlation at genetic level was moderate in NCWP2 and non-significant in NCW1.

Genotypic and phenotypic correlations between total fruit number and fruit size were significantly negative. Therefore, selection for more fruit per plant could result in small fruit size. Total fruit weight and marketable fruit weight showed a strong negative correlation with percent culls at both genotypic and phenotypic levels. In most cases, genotypic and phenotypic correlations were consistent across two populations. However, these estimates may vary with population since genotypic correlations are a function of gene frequencies (Bohren et al. 1966), as well as the testing environment and the breeding design used.

The distribution of S_0 individuals and $S_{0.1}$ family mean did not show discrete classes on the basis of Shapiro and Wilk's test (data not shown). Heritability estimates varied with location and population. Estimates of additive genetic variance varied between populations since they were a function of allelic frequencies. Thus, different values of heritability resulted.

NCWP2 had higher estimates of narrow-sense heritability for yield traits compared with NCWP1 when averaged over locations. Although both populations were developed from a similar set of cultivars, the methods of development differed. There was more recombination in the development of NCWP2 since the F_1 s were allowed to open-pollinate for the production of S_0 seeds. Thus, both populations were likely to have different allele frequencies. Moreover, the two populations were tested in different years. Estimates of narrow-sense heritability were low (0.04 for NCWP1, 0.12 for NCWP2) for total fruit weight in both populations of watermelon (Table 2). Low estimates for narrow-sense heritability indicated that a small proportion of total fruit weight was controlled by additive gene action, and multiple genes were involved. Gain can be achieved from selection in such cases, but it will be more difficult. Relatively higher gain in fruit weight can be expected in NCWP2 than NCWP1 based on higher heritability estimates. Similarly, low narrow-sense heritability was estimated for marketable fruit weight, 0.06 in NCWP1 and 0.15 in NCWP2. Estimates of narrow-sense heritability of total fruit number were 0.04 in NCWP1 and 0.16 in NCWP2. Fruit size (0.18 in NCWP1, 0.19 in NCWP2) had slightly higher heritability than fruit yield. Gusmini and Wehner (2007) recorded low to intermediate

Table 3 Predicted response and response to indirect selection (*italicized*) for trait Y based on selection for trait X at 10% selection intensity

Correlated traits (Y)					
Selected trait (X)	Total fruit wt. (Mg ha ⁻¹)	Total fruit no. (ha ⁻¹)	Mark. Fruit wt. (Mg ha ⁻¹)	Fruit size (kg)	Percent culls (% by weight)
<i>NCWP1</i>					
Total fruit wt. (Mg ha ⁻¹)	1.94 ^a	-7.04	2.25	0.24	-0.40
	<i>3.97^a</i>	<i>284.26</i>	<i>5</i>	<i>0.16</i>	<i>-3.14</i>
Total fruit no. (ha ⁻¹)	-0.04	352.04	0.07	-0.27	-0.22
	<i>0.45</i>	<i>498.65</i>	<i>2.00</i>	<i>-0.46</i>	<i>-5.30</i>
Mark. fruit wt. (Mg ha ⁻¹)	2.31	12.93	2.84	0.25	-0.77
	<i>3.12</i>	<i>459.69</i>	<i>3.73</i>	<i>-0.03</i>	<i>-1.87</i>
Fruit size (kg)	2.72	-552.62	2.65	0.79	0.31
	<i>2.16</i>	<i>-300.48</i>	<i>1.85</i>	<i>0.50</i>	<i>1.03</i>
Percent culls (% by weight)	-0.52	-333.57	-0.98	0.04	0.74
	<i>5.13</i>	<i>30.87</i>	<i>9.11</i>	<i>0.07</i>	<i>-16.40</i>
<i>NCWP2</i>					
Total fruit wt. (Mg ha ⁻¹)	3.66	241.17	3.95	0.38	-4.32
	<i>3.64</i>	<i>91.96</i>	<i>4.54</i>	<i>0.18</i>	<i>-2.01</i>
Total fruit no. (ha ⁻¹)	1.31	898.33	1.82	-0.55	-2.87
	<i>9.09</i>	<i>1414.36</i>	<i>7.89</i>	<i>-0.29</i>	<i>2.30</i>
Mark. fruit wt. (Mg ha ⁻¹)	4.10	347.92	4.41	0.35	-4.69
	<i>3.88</i>	<i>-154.69</i>	<i>4.59</i>	<i>0.38</i>	<i>-2.81</i>
Fruit size (kg)	2.44	-655.88	2.19	0.98	0.93
	<i>-0.21</i>	<i>-1118.49</i>	<i>-0.27</i>	<i>1.14</i>	<i>0.01</i>
Percent culls (% by weight)	-4.25	-518.78	-4.44	0.14	2.79
	<i>-4.96</i>	<i>965.55</i>	<i>-2.55</i>	<i>-1.62</i>	<i>-3.56</i>

Values are absolute change predicted in offspring

Predicted response ($PR_{y, x}$): $kr_g h_y h_x \sigma_y$

Response for indirect selection was based on selection of top 10% parents from raw data. Response is realized in offspring generation

^a Values in normal font indicate direct selection response for trait Y

levels of heritability for fruit size. Similar results were also reported in muskmelon (Moon et al. 2004). Percent culls had low estimates of narrow-sense heritability should probably be considered non-heritable. If culls were ignored, time and labor for recording cull fruit could be saved.

Broad-sense heritability (per-plot basis) was also estimated using $S_{0,1}$ progeny data (Table 2). Estimates were higher for NCWP2 than NCWP1. However, estimates of broad-sense heritability were inflated because of confounding of the $G \times E$ component of variance with genetic variance. Estimates of realized heritability were close approximations of narrow-sense heritability because the slope of the regression line estimates both narrow-sense and realized heritability.

Predicted gain from selection was calculated using both narrow-sense and realized heritability (Table 2). Total fruit weight was predicted to increase by 1.94 Mg ha⁻¹ in NCWP1 to 3.66 Mg ha⁻¹ in NCWP2 per cycle. Predicted gain for yield was 2 to 5% per selection cycle. Favorable genes would be accumulated over generations. Similarly, predicted gains for fruit number and marketable fruit weight were low because of their low heritability. Fruit size was predicted to increase 10 to 11% per cycle of selection. In some cases, realized gains from selection were similar to predicted gain (Table 2).

Marketable fruit weight and fruit size as selection criteria produced the best predicted response in total fruit weight in NCWP1 (Table 3). High genotypic

correlation of total fruit weight with marketable fruit weight and fruit size caused high predicted response (Table 1). However, in NCWP2, only marketable fruit weight as a selection criterion produced higher total fruit weight. Response to indirect selection was calculated by selecting 10% superior parental individuals and response was evaluated in the offspring (Table 3). In the NCWP1, total fruit weight as a selection criterion produced the highest marketable weight, whereas in the NCWP2, total fruit number as a selection criterion yielded the highest total and marketable weight.

Conclusions

Genotypic and phenotypic correlations among traits estimated in this study indicate characters that may be useful in selection. This information is valuable for reducing the number of traits to be evaluated in a watermelon breeding program. Total fruit weight and marketable fruit weight were highly positively correlated. Thus, the efficiency of a breeding program can be increased by measuring marketable fruit weight, because it will reliably predict total fruit weight. Marketable fruit weight had a high positive correlation with fruit size. Thus, fruit size would have to be monitored while selecting for yield. Fruit number was negatively correlated with fruit size, indicating that selection for more fruit would result in smaller fruit. Total fruit weight was negatively correlated with percent culls.

The results of this study confirm that watermelon yield has a low heritability. This finding indicates that yield is a complex trait and is controlled by multiple genes. Based on parent-offspring regression and the resulting estimates for yield, selection using single-plant hills would not be effective. A breeding scheme allowing maximum recombination would be useful, and recurrent selection for high yield should be effective. Fruit size had higher heritability than the other yield traits; this was consistent across populations. It should be possible to change fruit size rapidly through direct selection. Low to intermediate heritability would require the use of replicated progeny rows tested in multiple environments.

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