

Influence of Inflated Heritability Estimates on Gain of Selections in Early Generations of Spring Wheat *Triticum aestivum*

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Abstract. Nine lines, 16 F₂ and 16 F₃ families of spring wheat were used in this study. The nine lines differed in plant height (tall, medium and short), number of spikes/plant and grain yield/plant. Crosses were made among lines. The segregating generations (16 F₂ and 16 F₃) were also obtained and evaluated on single spaced plants. Heritability estimates in broad sense for plant height, spike no./plant and grain yield/plant were obtained from variance of F₃ mean and from offspring-parent regression coefficients. Estimates of heritability from variance of F₃ mean were found to be influenced by within family variance and were greater than that estimated from regression coefficient. Consequently, predicted gains were inflated from heritability estimates from variance components. Insignificant correlation was found between plant height and spike no./plant. Significant positive correlations were estimated between plant height and yield, and between spike no./plant and yield. Combinations of plant height with different yielding ability were obtained in F₃ families and reasonable gains from selection were obtained for the studied traits. Selection of medium stature plant with higher yield would be effective.

Introduction

During the early segregating generations of crosses, a genotype possessing the desirable gene(s) either homozygous and/or heterozygous which largely occur in the F₂ generation since the frequencies of desirable segregating genotypes will decline in subsequent generations. Selection for desirable traits in early-segregating generations of wheat *T. aestivum* has been practiced by many investigators. They were able to identify and use lines with desirable traits that could combine high yield with desirable trait(s). McVetty and Evans [1 and 2] determined characters which were measured on F₂ spaced plants to identify high-yielding F₄ in bulks. They found that most of the studied characters were significantly correlated with F₄ bulk yields. However, several breeders found that selection for yield and/or yield potential using single

plants in early generations (F2 or F3) within crosses were ineffective, [3 and 4]. However, yield components, harvest index or combinations have been suggested as criteria for selection in early generation of wheat, [5 and 6].

Meanwhile, Smith and Nelson [7] used early estimates of reproductive growth period to predict yield in soybean. Heritability estimates, simple regression, stepwise multiple regression and correlations have been used to predict yield improvement in early generations, [1, 7 and 8].

This investigation aims at: (1) Identifying lines with high yielding potential, combined with short and/or medium height in early generation. (2) Predicting progress after selection for desirable character(s) with high yielding ability. (3) Estimating inflation in heritabilities and expected progress that could mislead selections in early-generations. (4) Identifying the constancy of characters in advanced generations. (5) Studying the relationships between plant height, spike no./plant and grain yield/plant.

Materials and Methods

The nine bread wheat genotypes used in this investigation were (1) HD.2203, (2) CA.6194, (3) L.S.130, (4) PESIGAON, (5) HD.2206, (6) SAKHA 69, (7) HD.2172, (8) CM.35630, and (9) KASIOUN. All have had different origin and exhibit differences in plant height (from 85 cm - 141 cm) and grain yield (16 g/plant - 30 g/plant), (Table 3). Crosses were made among these genotypes in 1987. Seeds of 16 different crosses (F1) were obtained. Seeds of the 16 F2 and 16 F3 were obtained in winter of 1988 and 1989, respectively. An experimental trial was conducted which included 9 parents, 16 F2 and 16 F3 families at the Agricultural Research Station in Deirab (24 N and 46 E) near Riyadh. The trial was a randomized complete block design with eight replicates. Each block considered of 45 plots. The plot consisted of two rows, 2 m long and spaced 20 cm apart. Planting date was November, 20, 1990. Conventional agricultural practices were applied during the growing season as recommended for wheat production in that area except that plants were covered with plastic tents during grain filling stage until maturity to avoid bird damages. At maturity, data were taken on single plant basis for the following characters: plant height measured in cm from ground to the tip of the spike, number of spikes per plant (NSP) and grain yield weight (GYW) in grams per plant. Average plant height, number of spikes/plant and grain yield/plant in each plot were also obtained for statistical analysis.

Statistical analysis was accomplished on mean plot basis using the SAS program V. 3.1 ANOVA among genotypes, coefficients of variation, and least square differ-

ences were obtained. The covariance of F3 mean with its F2 parents measured ($F3/F2 = 1/2D+1/8H$), [9, p. 382]. Regression coefficient (b) was obtained for each character and used as heritability estimate in broad sense. Moreover, genotypic, phenotypic variances were estimated for the F3 generation (S2) families. Genotypic coefficient of variation for a specific character was calculated as the square root of the genotypic variance divided by the mean of that character. Heritabilities in broad sense were calculated from (variance of F3 means ($V1F3$) which contains $= 1/2D+1/16H+E2$). The term E2 included in the variance of F3 mean is non-heritable variance and that is equal to $E_b+1/m E_w$ and $1/mE_w = 1/m(V2F3)$, where, E_b =variance between families, E_w = variance within family, and m is the harmonic mean of non equal numbers per family in this study, and $V2F3$ is the mean variance of F3 families [9, p. 382].

The expected genetic advance from selection \hat{g} ($i h \sigma_{ph}$) was calculated where, (i) is selection intensity of 5% for the desired character, (h) is heritability ratio and σ_{ph} is a phenotypic standard deviation. The predicted genetic advance \hat{g}/x was calculated as a percent of the population mean, [10].

Results and Discussion

Highly significant differences in plant height, number of spikes per plant and grain yield per plant were obtained among the nine parents and the 16 F2 families, (Table 1). Highly significant differences were also obtained for the studied characters in the 16 F3 families, (Table 2). Apparently, genetic differences within these populations may have contributed to the differences in plant height, spike number/plant and grain yield/plant among the nine parents and the 16 F2 families as well as among the 16 F3 families.

Table 1. ANOVA of plant height, number of spikes/plant and grain yield/plant for 9 parents and 16 F2 families of bread wheat grown in winter, 1991

Source of variation	d.f.	Mean of squares		
		Plant height	No. of spikes/plant	Grain yield per plant
Replication	7	134.12**	7.63 ^{ns}	57.40 ^{ns}
Genotypes	24	1710.68**	45.21**	140.17**
Error	168	28.91	7.98	27.53

ns and ** are insignificant and significant at 1% level, respectively.

Table 4. Means and least significant difference (LSD) values for plant height (cm), spike number and grain yield/plant of 16 F3 Families of bread wheat

F3 Families	Plant height	Spike No./plant	Grain yield/plant
HD.2203 × HD.2173	132.34 a	15.24 b-e	27.91 bc
L.S. 130 × HD.2206	129.67 ab	16.17 a-c	23.89 bcdef
L.S.130 × CM.35630	128.45 abc	11.46 g	19.69 ghf
PESIGAON × HD.2206	128.13 abc	16.73 ab	29.04 b
HD.2203 × CM.35630	125.72 bcd	15.51 b-d	27.03 bcd
HD.2203 × SAKHA 69	124.41 cde	16.82 ab	23.49 cdef
PESIGAON × CM.35630	123.74 cde	14.95 b-f	22.20 defg
PESIGAON × HD.2172	122.74 def	18.15 a	34.52 a
PESIGAON × KASIOUN	121.29 defg	18.53 a	28.88 b
HD.2203 × KASIOUN	120.14 efgh	12.98 e-g	23.40 cdef
CA.6194 × HD.2172	118.67 fghi	15.67 bc	26.44 bcde
CA.6194 × CM.35630	117.37 ghi	13.98 c-f	22.31 defg
CA.6194 × SAKHA 69	117.34 ghi	13.26 d-g	17.65 gh
CA.6194 × HD.2206	116.06 hi	12.83 fg	16.58 h
L.S.130 × KASIOUN	115.18 i	12.82 fg	21.45 efgh
CA.6194 × KASIOUN	113.88 i	14.85 b-f	16.82 h
Average	122.19	14.99	23.83
LSD	4.83	2.37	5.20

families (Tables 3 and 4). High number of spikes/plant was obtained from the cross of PESIGAON (a tall parent) with CM.35630 (a short parent) and that between PESIGAON and HD.2172 (a medium parent). However, most families in both F2 and F3 families which included the short parents (CM.35630 and KASIOUN) had lower number of spikes/plant. Meanwhile, all crosses that involved tall and medium height lines except that between L.S.130 × HD.2206 produced families in F2 and F3 generations with above average spike no./plant. However, insignificant correlation coefficient between plant height and spike number/plant was obtained ($r=0.074$), Table 5. Accordingly, plant height might not affect spike number/plant. On the contrary, dwarf genes had adverse effects on final stand (seedlings per plant) in wheat (*T. aestivum*) [13].

Grain yield per plant

Seed yield gram/plant ranged from 11.90 grams in the tall line CA.6194 which exhibited low number of spikes/plant to 26.42 grams in the tall parent HD.2204

which had high number of spikes/plant. The tall parent PESIGAON with high number of spikes/plant exhibited also high grain yield/plant (25.09 gram). The medium height lines, i.e., HD.2206, SAKHA 69 and HD.2172 produced 19.49, 19.96 and 24.83 grams of grains/plant, respectively; these lines produced high number of spikes/plant (Table 3). Moreover, yield of short lines that had low spike number was reduced to some extent. This could indicate the importance of spike number to determine grain yield. Correlation coefficient between spike number/plant and grain yield was ($r=0.67$) which was greater than that between plant height and grain yield ($r=0.25$) (Table 5).

Table 5. Simple correlation coefficients between plant height (HP), spike no./plant (SNP) and grain yield /plant (GYP) measured from parents, F2 and F3 populations

Characters	HP	SNP	GYP
Plant height (HP)	—	0.074 ^{ns}	0.25**
Spike no./plant (SNP)	0.074	—	0.67**
Grain yield/plant (GYP)	0.25**	0.670**	—

** significant at $p < 0.01$

Significant differences among the F2 families were apparent for grain yield/plant. Grain yield ranged from 18.6 gram/plant in the family L.S. 130 × KASIOUN (it has lower spikes/plant) to 29.95 grams/plant in the family PESIGAON × HD.2206 (Table 3). Nine families exhibited grain yield greater than the average (22.07 grams). Most of the high yielding families showed high number of spikes/plant. Accordingly, number of spikes/plant could be used as a criterion for selection of higher yielding plant(s) and/or families. Similar results were observed among the F3 families which produced higher grain yield/plant (Table 4). This finding could strengthen the constancy of high yielding families in successive selection generations and this was comparable to that found by some other investigators [3 and 6] in wheat. Moreover, McVetty and Evans, [1 and 2] found high significant positive correlation coefficient for different spring wheat parameters, i.e., between grain yield/plant and plant height; and between tiller number/plant and grain yield/plant.

Heritability and predicted gain

The variances, coefficient of variations, offspring-parent regression coefficient ($b \pm sb$), heritability estimates in broad sense, and predicted genetic advance from selection are given in Table 6. Phenotypic and genotypic coefficient of variations for

Table 6. Estimates of phenotypic variance (Phv), genotypic variance (Gv), coefficient of variations, heritability values and predicted genetic advance ($\Delta \hat{g}\%$) for plant height, spike no./plant and grain yield/plant in spring wheat

	Characters		
	Plant height (cm)	Spike No./plant	Grain yield/plant (gram)
Ph.V	52.40	9.09	48.68
G.V.	28.65	3.34	21.12
ph.C.V	3.99	15.98	22.02
G.C.V	4.38	12.19	19.28
Regres. coef. (b) \pm sb	0.53 \pm 0.15	0.26 \pm 0.08	0.17 \pm 0.07
Heritability (1) Broad (of variance)	0.55	0.37	0.43
Heritability (2) Broad (of regres.)	0.53 \pm 0.15	0.26 \pm 0.08	0.17 \pm 0.07
$\Delta \hat{G}\%$ (1), (5%)	4.50%	12.19%	19.50%
$\Delta \hat{G}\%$ (2), (5%) (of regression)	4.35%	8.56%	7.70%

Where, $h_2(1)$ heritability in broad sense estimated from variance of F3 mean (VIF3); $h_2(2) = (b)$ offspring-parent regression coefficient, sb =standard error of regression coefficient, $\Delta \hat{G}(1)$, is percent genetic advance from selection of 5% plants using heritability values from variances, and $\Delta \hat{G}(2)$, 5% = percent genetic advance using heritability estimates of offspring parent regression coefficients.

plant height in F3 were 3.99% and 4.38%, respectively. Meanwhile, coefficient of variations, i.e., phenotypic and genotypic were high for spike no./plant (15.98 and 12.19, respectively) and grain yield/plant (22.02 and 19.28, respectively). Therefore, high variabilities were found among the F3 families for these traits and selection would be effective. The regression coefficient of offspring on parents (b) is equal to parent progeny covariance divided by the parents phenotypic variance. The value of (b) was used as heritability value in broad sense. Hence, the parent-offspring covariance contained the following proportions: $6op = 6Gop + 2\ 6GEop + 6Eop$. Where, $6op$ and $6Gop$ are the phenotypic and genotypic covariance between offspring and parent; the symbols $6GEop$ and $6E$ refer to covariance between genotypic and environment, and environmental covariance between parents and offspring, respectively. Since the families were randomized, therefore, the families and the environment were not correlated and the symbol $2\ 6GEop$ should be set to zero.

Moreover, the F₂ and F₃ families (parent and progeny) were likewise randomized to different plots (were not included in the same plot), therefore the value $6E_{op}$ has to be equal to zero. Therefore, $COV_{op} = 6\sigma_p = 6\sigma_{Gop} = 1/2 \sigma_A^2 + 1/8 \sigma_D^2$ (additive) + $1/8 \sigma_D^2$ (dominance [14, pp. 225-246] [and 9]). However, heritability estimates for the studied characters in this work might be biased upward only by the small dominance variance and dominance variance interactions. Meanwhile, the additive X additive (epistatic variance) is considered to be fixed like that of the additive variance and useful in selection of desirable traits.

Contrarily, heritability estimates from variance of F₃ mean is equal to $VIF_3 = 1/2 \sigma_A^2 + 1/16 \sigma_D^2 + \sigma_{Eb} + 1/m \sigma_{Ew}$, likewise A and D are the additive and dominance variances, respectively, σ_{Eb} = nonheritable variance due variance between families, and σ_{Ew} = nonheritable variance due to variance within families [9]. Since, the F₂ plant will segregate to give F₃; families, one would expect that the term σ_{Ew} would be large, meanwhile, a small portion will be maintained in the mean square of error variance in the analysis of variance of F₃ (Table 2). Moreover, the analysis of variance did not permit of estimate within family variances because data were handled on average mean basis of plant/plot. Therefore, heritability estimates would be upward biased because the σ_{Ew}^2 (variance within families) is not included in the denominator (phenotypic variance) of heritability estimate [15, pp. 41-74].

Heritability estimates from variance components were (0.55) for plant height, (0.37) for spike no./plant and (0.17) for grain yield/plant. These estimates were greater than those estimated from regression coefficient, which were 0.53, 0.26 and 0.17 for the same characters, respectively (Table 6). Moreover, predicted genetic gain % (using selection intensity of 5% were greater when heritability from variance estimates were used as compared with those of regression coefficient, i.e., 4.5% > 4.35 for plant height; 12.19 > 8.56 for spike no./plant and 19.50 > 7.70% for grain yield/plant, respectively (Table 6). The expected progress is consequently upward biased when the employed heritability estimates were from variance components but not from regression coefficients in this experiment.

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تأثير حساب درجة التوريث على التقدم الانتخابي لبعض الصفات في الأجيال المبكرة في القمح الربيعي

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ملخص البحث. شملت الدراسة ٩ سلالات من القمح، ١٦ عائلة ناتجة من التهجين بينها لكل من الجيلين الثاني والثالث. وكانت السلالات مختلفة فيما بينها بالنسبة لصفة طول النبات. وقسمت إلى ثلاثة مجاميع (طويل، متوسط، قصير) كما كانت تختلف فيما بينها بالنسبة لصفة عدد السنايل للنبات ومتوسط محصول البذور للنبات.

قومت عائلات الجيلين الثاني والثالث للصفات الثلاث وتم حساب درجة التوريث في المدى الواسع باستخدام مكونات التباين للمتوسط للجيل الثالث وكذلك باستخدام معامل الانحدار (b) للنسل - الآباء (F2/F3). وكانت درجة التوريث المحسوبة من تباين الجيل الثالث متضخمة عن تلك المحسوبة من التباين المشترك (معامل الانحدار)، وبالتالي كان التقدم الانتخابي عند ٥٪ متضخماً أيضاً عند استخدام درجة التوريث من تباين الجيل الثالث عنه عند استخدام معامل الانحدار في حساب التقدم الانتخابي الوراثي. كان معامل الارتباط الظاهري بين طول النبات وعدد السنايل للنبات غير معنوي بينما كان هناك ارتباط معنوي بين طول النبات والمحصول وكذلك بين عدد السنايل والمحصول للنبات. وكانت هناك توافقات مختلفة بالنسبة لصفة طول النبات وصفات المحصول الأخرى في الجيل الثالث. وأوضحت الدراسة أن التقدم الانتخابي يكون مجدياً للصفات المدروسة - كما أن الانتخاب للنبات متوسط الطول من ذوي المحصول العالي يكون مجدياً.

