EFFECTS OF SELECTION FOR KERNELS PER SPIKE IN TWO

POPULATIONS OF WINTER WHEAT

By

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EFFECTS OF SELECTION FOR KERNELS PER SPIKE IN TWO

POPULATIONS OF WINTER WHEAT

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CHAPTER I

INTRODUCTION

Throughout history, advances in crop production have been cyclic in nature. Each advance is brought about by the application of new technology. However, with each advance, new problems are encountered. Today, with the dramatic growth in world population, the demand for available food is fast exceeding our present level of productivity. Improvements in the yield of wheat, which is the most important cereal grain in the world, may help offset this situation.

Grain yield in wheat is a very complex character which is difficult to select for in early generations. Higher levels of success might be achieved through the selection of one or more of the major components of yield (i.e. kernel weight, kernels per spike, or tiller number) as opposed to the selection for yield itself. One of the problems encountered in selection for yield components is the negative relationship which often exists between components. As one component is increased there is a tendency for one or more of the other major components to decrease. Therefore, in order to improve overall yield, gains made in any one component through direct selection must exceed the characteristic decline in the others.

The number of kernels per spike is one of the components of yield and is of particular interest in this study. Theoretically, it should be more amenable to selection than yield itself in a breeding program.

The objectives of this study were (1) to determine the effectiveness of selection for increased kernels per spike in improving yield in wheat, (2) to estimate the heritability of the kernels per spike characteristic, (3) to calculate the genetic correlations among grain yield, kernels per spike, kernel weight, and plant height, and (4) to utilize a grid selection technique with kernels per spike to determine the effectiveness of this procedure.

CHAPTER II

LITERATURE REVIEW

Increasing yield potential is a major objective of most breeding programs today. Early generation selection for yield would be desirable because it would improve the overall efficiency of a breeding program. However, yield is a quantitative trait of low heritability which traditionally has not been amenable to selection in early generations. Several researchers have found that selection for yield potential based on single plant performance in early generations (F_2 or F_3) is inefficient (3, 22, 25). Johnson et al. (18) suggested that as yields are pushed higher, new levels of productivity become increasingly difficult to attain and that attention to the expression of individual components of yield could provide a better basis for selection of parents and for evaluation of their progenies than yield itself.

Grafius (12) presented a geometrical interpretation of yield. Using his model, yield may be considered as a volume with the edges being represented by the different components of yield. Grafius proposed that the greatest potential for improving the yield of a cultivar is to be found in the increase of the shortest edge (limiting component). Many wheat breeding programs have subsequently adopted similar philosophies, in that major emphasis is being placed on yield components. In wheat the ultimate goal is to find the best balance of the three yield components: tiller number, kernels per spike and kernel weight. In striv-

ing for this goal, direct selection for yield components provides a means of indirect selection for yield itself.

Successful yield component selection is dependent upon the degree of heritability, the interrelationships among components and between components and yield (34, 35). Hanson (15) pointed out that heritability estimates are dependent on the methods of estimation and measurement, generation of hybrid, and environmental factors. Although the effectiveness of indirect selection for yield, as with heritability estimates and other genetic parameters, seems to be specific to individual crosses or populations and the environments in which they are grown, the accumulation of these types of estimates from diverse studies provide general trends or patterns. These patterns can aid the breeder in understanding the inheritance of particular traits and their interrelationships.

In practice, indirect selection for yield based on yield components has shown varied results. Yield components in wheat often show compensating effects and negative intercomponent correlations in which any gain in a single component may be offset by decreases in one or both of the other components, producing no net gain in total yield. Busch and Kofoid (4), working in spring wheat, screened 200 lines for kernel weight and selected the best ten. The ten selected lines were intercrossed and selections based on kernel weight were made in the next three cycles. They reported a significant increase in kernel weight over the three cycles of selection. Selection for kernel weight increased spike length but reduced kernels per spike and kernels per spikelet. The reduction in kernels per spike and kernels per spikelet offset the gains in kernel weight and spike length, resulting in no increase in yield. Adams (1) explained that negative associations among yield components general-

ly occur as the result of competition for metabolites between genetically independent and sequentially developing yield components.

A plant ideotype method of breeding has been proposed by Donald (7). Using this concept, yield-related traits rather than yield per se are emphasized in the breeding program. These traits are identified, selected for, and ultimately combined into a single genotype in which yield components are balanced for the maximum expression of yield in a given environment. Smith (35) presented a plant architecture model which represented his concept of the hard red winter wheat ideotype for the Southern Great Plains of the United States. He postulated an optimum level of expression for each trait in the model and suggested that it should be possible to improve grain yield potential by increasing one of the yield components while holding the others constant.

Grafius and Weibe (14) stated that breeders should ignore components with low heritability and concentrate on those having the highest values. That is to say, that selection for yield components should be based on the expected genetic gain for those components. Selection, therefore, should be made for those components with high heritabilities and subsequent high expected genetic gain.

Several studies have shown that selection for increased kernel weight in wheat is perhaps the most effective means of improving yield through indirect selection (21, 26, 30, 34). In a study by Sidwell et al. (34), kernel weight was the only yield component to display high narrow-sense heritability values. On the basis of heritability values, direct selection to improve kernel weight should be more effective than for any other trait studied. They found that while tiller number made a greater contribution toward grain yield, it would be much more diffi-

cult to improve by selection in early generations because of low heritability values.

Spike size, or number of kernels per spike, is one of the major components of yield. According to Smith's (35) plant architecture model, this trait should receive prime consideration. Schmidt (32) stated that Turkey-type cultivars, common to the Southern Great Plains, are characteristically low with regard to kernels per spike and there are indications that an inhibitor of spike fertility may exist in these types not found in the more modern cultivars from the Far East or Europe.

Reported heritability estimates of kernels per spike vary widely. Fonesca and Patterson (9), using a seven-parent diallel cross of winter wheat, found kernels per spike heritability estimates of $0.47 \pm .16$ and $0.89 \pm .08$ for F_1 hill plots and $0.85 \pm .18$ for F_2 drilled plots. Paroda and Joshi (30), in a six-parent diallel cross of spring wheats, found high heritabilities for both kernel weight and kernels per spike. In a combining ability study, Kronstad and Foote (23) estimated narrow-sense heritability using parent-progeny regressions on space-planted F_1's in a ten-parent diallel cross of winter wheat. They found that spikelets per spike and kernels per spikelet both had higher narrow-sense heritabilities than kernel weight with estimates of 0.61, 0.48, and 0.47, respectively. Low narrow-sense heritability estimates for kernels per spike were reported in separate studies by Sidwell et al. (34) and Ketata et al. (20). Both studies utilized space-planted parents, F_1, F_2, and first generation backcrosses.

Genotype X environment interaction may bias heritability estimates as reported in a study conducted by O'Brien et al. (29). The ratio of observed response to the selection differential or realized heritability

may be used to remove this bias. Dhanasobhon (6) studied three populations of winter wheat in the F_2, F_3, and F_4 in succeeding years. She found that in all three populations studied, realized heritability estimates of yield were high to intermediate and exceeded those of the yield components using F_3 and F_4 response to F_2 selection. These results were not consistent with previously reported heritability estimates (17, 23, 27). However, Dhanasobhon's (6) realized heritability coefficients based on response in F_4 from F_3 selection were more in line with reports by Smith (35) and others (17, 23, 27). She reasoned that heritability based on response in F_4 from selection in F_3 was more reliable because mean values of measured characters in both F_3 and F_4 were based on replicated plot averages while the F_2 values were based on single plant values. Dhanasobhon found kernels per spike in the F_4 - F_3 response-selection system to have realized heritability coefficients of 0.48, 0.59, and 0.72 for the three respective populations under study. Kernels per spike ranked second only to kernel weight in magnitude of heritability.

In a winter wheat cross, Sidwell (33) calculated realized heritability based on an F_3 - F_2 response-selection system. He also found that the realized heritability estimate for kernels per spike was second only to kernel weight in order of magnitude.

As was stated previously, little benefit can be seen in selection for a highly heritable trait if gains for that character are offset by the reduction of one or more other traits. It is necessary to have a good understanding of the interrelationships among plant traits before an efficient selection program can be established. Several workers have investigated the relationships of yield components to overall yield

in wheat. In several studies, kernel weight generally had an intermediate to high phenotypic correlation with yield that was positive in sign (9, 26, 34); however, Ketata et al. (19) found a low, positive correlation between these two traits. Ketata et al. (19), Larkins (24), Sidwell et al. (34) and McNeal (26) found high, positive phenotypic correlations between tiller number and yield. An intermediate, positive correlation for this trait was reported by Fonesca and Patterson (9). Sidwell et al. (34) reported that kernels per spike had a low, positive phenotypic correlation with yield but had a genetic correlation of intermediate magnitude with that trait. Gill et al. (11) found a high, positive phenotypic correlation between kernels per spike and yield in wheat. This is in agreement with work by Larkins (24) who found a moderately high correlation between these two traits.

Interrelationships among yield components themselves have been reported by several researchers. Larkins (24) found positive correlations, low in magnitude, between tiller number and the other two components. Kernels per spike had an intermediate, negative correlation with kernel weight in a study conducted by Cammack (5). Fonseca and Patterson (9) reported negative correlations of intermediate magnitude between kernels per spike and kernel weight, and between kernels per spike and tiller number.

Yield components are known to be highly influenced by environmental effects. This was borne out in a study on winter wheat by Johnson et al. (17). Several workers have suggested techniques which would aid in reducing environmental error, thereby making selection more effective. Nass (28) suggested that environmental differences can be reduced by selecting wheats under high population density. Selection for high yield

would then be based on superior head weights. Gardner (10), working in maize, devised a modified form of mass selection in which his selection block was stratified into equal-sized grids and an equal number of plants were selected from each grid. The effectiveness of selection, he reasoned, would be increased if the amount of environmental variation among those plants being compared for selection was reduced. Verhalen et al. (37) tested a stratified grid method of selection in cotton against an identical selection procedure without grids. They found that the grid method reduced phenotypic variation by 22% and increased selection responses by 20 to 35%. Realized heritability estimates were 40 to 52% higher than those for the identical selection procedure without grids. Verhalen et al. (37) stated that the stratified grid system should increase the effectiveness of selection regardless of the crop, quantitative trait, or breeding method employed, provided there is genetic and environmental variability in the material.

Several workers have noted that kernels per spike is a character of potential usefulness in terms of indirect selection of yield (13, 18, 24, 27, 34, 35). Most wheat cultivars grown in the Southern Great Plains area tend to be lacking in number of kernels per spike. By selecting for increased values for this trait, overall grain yield would be increased provided the other components of yield could be maintained at a relatively constant level.

CHAPTER III

METHODS AND MATERIALS

Materials

Fifty-six F_3 progeny rows for each of two populations of winter wheat (Triticum aestivum L. em Thell.) were studied at the Agronomy Research Station, Stillwater, during the 1979-80 crop season. The two populations originated from crossing a common germplasm line, 'Fundulea 23-71' or F 23-71, to 'Caprock' (Population 1) and 'TAM W-101' (Population 2). Caprock and TAM W-101 are both adapted to the Southern Great Plains and are grown commercially in Oklahoma.

F 23-71 was developed at the Fundulea Station, Romania, by crossing Neuzucht (a German breeding line) with F 362-62 (a Romanian breeding line). F 23-71 is a winter wheat characterized by large spikes, medium-sized kernels, tall stature, and late maturity. It has the highest value for number of kernels per spike of all genotypes so far examined in the Oklahoma wheat breeding program (36).

Caprock is a hard red winter wheat which was released by the Texas Agricultural Experiment Station in 1969. Caprock was selected from the cross 'Sinvalocho'/'Wichita'/2/'Hope'/'Cheyenne'/3/Wichita/4/'Seu Seun 27'. It is characterized by medium-sized kernels, short straw, early maturity, and good milling and baking qualities (2).

TAM W-101 was released by the Texas Agricultural Experiment Station in 1971. It is a hard red winter wheat selected from the cross 'Norin

16'/3/'Nebraska 60'//'Mediterranean'/Hope/4/'Bison'. TAM W-101 is characterized by relatively large kernels, short straw, medium maturity, and good yield potential (31).

F_2 Populations and Selection

In the 1978 crop year, Larkins (24) studied a total of 256 F_2 plants from each of the two populations described above. In his study, each population consisted of 16 grids or sets, each containing 16 bordered F_2 plants with a 30 cm spacing between plants. Larkins (24) measured 16 individual F_2 plants per grid for kernels per spike, kernel weight, grain yield, and plant height.

Based on Larkins' (24) measurements, a stratified grid method of selection for high and low kernels per spike was used to obtain the material for this study. Within certain minimum standards, the two plants with the highest values for kernels per spike and the two plants with the lowest values for this trait were selected from each of 14 of Larkins' 16 grids. To guard against extremely poor F_3 progeny rows, the minimum standards were: (1) 25 kernels per spike, (2) 1000 kernel weight of 29.0 g, and (3) an average spike yield of at least 0.8 g.

Field Layout of F_3 Progeny Rows

The experimental design was a split plot with three replications. Each population consisted of 14 main plots. Each main plot traced to a grid in Larkins' (24) study and was made up of four sub-plots (the two high and two low progeny rows from selected F_2 plants). The respective parents and two check cultivars, 'Scout 66' and 'Newton', were sub-plots in the 15th main plot of each population. These parent/check main plots

were included to provide a gauge for extreme environmental conditions which might affect the populations as a whole. Each sub-plot was a single row 1.33 m in length with 30 cm spacing between sub-plots (rows).

The study was planted October 27, 1979 on a Norge loam soil type (Udic Paleustoll). Plots were seeded with a tractor-mounted cone planter at a rate of 50 sound seed/sub-plot. No preplant application of fertilizer was made, but on March 3, 1980, a top-dressing of ammonium nitrate was applied at the rate of 37 kg/ha actual N. Sub-plots (rows) were harvested (1 m length of each row) on June 24, 1980, using a hand sickle and a measuring stick. Each harvested bundle was bound, bagged, and later threshed with a Vogel nursery thresher.

Characters Evaluated

The number of kernels per spike, kernel weight, grain yield, plant height, and heading date were evaluated in this study. Measurements were made for each sub-plot in all three replications. The characters were measured in the following manner.

Kernels/spike

Three upper-story spikes were taken from each sub-plot. The three spikes were threshed in bulk and the number of kernels counted and divided by three to determine the average number of kernels per spike.

Kernel Weight

Kernel weight was determined by dividing the grain weight of the three selected spikes by the number of kernels produced in those spikes. This was expressed as grams per 1000 kernels.

Grain Yield

The weight of the three selected heads was added to the weight of the threshed grain from each sub-plot for total grain yield. This trait was expressed in g/plot.

Plant Height

Plant height was measured as the distance, in centimeters, from the soil surface to the tip of the average upper story head (excluding awns) in each sub-plot.

Heading Date

Heading date was expressed as the number of days after March 31, when, by visual estimation, 50% of the plants in a sub-plot were fully headed.

Statistical Analyses

An analysis of variance was conducted on the F_3 progeny rows for each character to detect the presence or absence of significant differences among main plots and between selection types. The difference between the means of the high selection group (H) and those of the low selection group (L) was calculated for each of the five characters measured to determine the direct and indirect effects of selection for number of kernels per spike. A test of mean differences for each character was provided by the selection type (H vs L) source of variation in the analysis of variance. Realized heritability for the kernels-per-spike character was calculated using a formula derived from Falconer (8). This will be discussed in further detail in Chapter IV.

Four agronomic traits were measured in common in the F_2 and F_3 populations. These were kernels per spike, kernel weight, grain yield, and plant height. The regression of F_3 rows on F_2 plants was conducted for each trait, providing an estimate of heritability for these four characters. Using a regression technique suggested by Hazel (16), genetic correlations among the four traits were calculated.

The fundamental basis for stratified grid selection is the reduction of environmental variation among plants being considered for selection. An analysis of variance was conducted on Larkins' F_2 data (all 256 plants per population) to determine the among-grid-component (σ_A^2) and within-grid-component (σ_W^2) of the total phenotypic variance (σ_T^2), where $\sigma_T^2 = \sigma_A^2 + \sigma_W^2$.

The ratio of response from grid selection (R_W) to that of selection without grids (R_T) is equal to the ratio of the standard deviation of the total population (σ_T) to the standard deviation within a grid; thus

$$\frac{R_W}{R_T} = \frac{\sigma_T}{\sigma_W} = \sqrt{\frac{\sigma_A^2}{\sigma_W^2} + 1} \ .$$

Through use of this formula the relative efficiency of grid selection was compared to that of selection without grids.

Statistical analyses were conducted at the Oklahoma State University Computer Center with assistance provided by the Department of Statistics faculty.

CHAPTER IV

RESULTS AND DISCUSSION

Analyses of Variance

Mean squares from F_3 progeny rows for the five traits of Populations 1 and 2 are shown in Tables I and II respectively. In Population 1 (F 23 -71/Caprock) there were significant differences among main plots for kernel weight, plant height, and heading date, but not for kernels per spike or grain yield. Highly significant differences among main plots (0.01 probability level) were observed for all five characters in Population 2 (F 23-71/TAM W-101). This source of variation is a measure of the mean differences in response evoked by the four F_3 progenies in one main plot as compared to another.

The selection-type (H vs L) source of variation measures the difference between the overall average of the high selections and that of the low selections. Differences between selection-types were highly significant for kernels per spike and grain yield in both populations. The implications of these differences between selection-types for these two traits will be discussed in the following section. Selection-type means squares were not significant for kernel weight, plant height, or heading date in either population.

The only significant (0.05 probability level) main plot selection-type interaction was that observed for heading date in Population 1. The lack of significant differences for this source of variation suggests

that the selection response for all of the measured characters was consistent, with the exception of this one case.

The variance of sub-plots within main plots and selection-type was highly significant for all traits in both populations, with the exception of kernels per spike in Population 2, which was significant at the 0.05 level of probability.

Mean Comparison and Effects of Selection
for Kernels per Spike

High and low selection-type means for each character measured in Populations 1 and 2 are presented in Tables III and IV respectively. The mean difference between selection-types was calculated and converted into percentages of the high selection-type mean values for each character. The test of significance of mean differences was provided by the selection-type source of variation in the analysis of variance.

In both populations a highly significant difference was observed between selection-types for the kernels per spike. This difference was 15.6% or approximately eight kernels per spike in Population 1, and was 15.0% or approximately seven kernels per spike in Population 2. Highly significant differences between selection-types for grain yield of 24.7 and 28.6% were observed in Populations 1 and 2 respectively. These differences were equivalent to 26.12 g/plot in Population 1 and 35.66 g/plot in Population 2. No other character in either population displayed significant differences between high and low selection-types.

Since each sub-plot was an F_3 progeny tracing to a selected F_2 plant, the data presented in Tables III and IV may be viewed in terms of a selection-response system. Selection for high and low kernels per spike in

the F_2 resulted in highly significant direct response differences in kernels per spike in the F_3. Highly significant indirect responses for grain yield in the F_3 were observed from selection for number of kernels per spike in the F_2. Because there was no significant change in kernel weight in either population, selection for increased kernels per spike proved to be an effective means of increasing overall grain yield. This is in agreement with McNeal et al. (27) and others (18, 24).

Means

The means of the ten highest yielding F_3 progenies of Populations 1 and 2 are listed in Table V in order of rank. The mean values for kernels per spike, kernel weight, plant height, and heading date are also given. Differences between the two populations can be seen by comparing the F_3 progeny means for these five traits.

Population 2 sub-plots tended to have higher grain yields with a mean value of 107.0 g/plot, while Population 1 had a mean grain yield value of 92.8 g/plot. The mean of Population 1 for kernels per spike exceeded that of Population 2 (49.0 and 44.7 respectively). The mean for kernel weight was 31.7 g/1000 in Population 1 and 34.8 g/1000 in Population 2. Population 1 had a mean plant height of 100.7 cm and a mean number of days to heading of 41.2. Population 2 was slightly taller and later, with a mean height of 104.7 cm and mean number of days to heading of 42.2. Larkins (24) noted a higher tillering capacity in the F_2 for Population 2 as compared to Population 1. The higher mean kernel weight of Population 2 and its noted higher tillering capacity seem to have offset the lower mean number of kernels per spike and probably account for the superior grain yield mean of Population 2.

Entry 54008-2 of Population 1 (Table V) was classified as a low selection-type line but exceeded the population mean for number of kernels per spike by a substantial margin (56.3 vs 49.0). This was probably a case of misclassification in the F_2. All other high yielding entries in both populations were high selection-type progenies.

F 23-71 displayed the highest mean number of kernels per spike in both populations with mean values of 65.7 and 60.3 for Populations 1 and 2 respectively. Entry 54006-15 of Population 1 was the only F_3 line in the top yielding entries which displayed an equivalent mean number of kernels per spike (65.3). The means of both populations exceeded those of the adapted parents for all traits measured. However, the mean yield of TAM W-101 as well as that of the Newton check was much lower than expected. Based on past performance TAM W-101 and Newton traditionally have 20 to 25% higher yields than that of Scout 66 (36). This departure from past performance may have been the result of a shading effect on these two semi-dwarf cultivars.

Heritability Estimates

Heritability was estimated by two different methods for kernels per spike, i.e. by calculated realized heritability using selection-type differences and by regression of F_3 values on F_2. Heritabilities determined by regression were also made for grain yield, kernel weight, and plant height. Heritability estimates are presented in Table VI.

Realized heritability is an estimate of the effectiveness of selection in one generation based on performance or response in a following generation. Falconer (8) defines realized heritability as the ratio of response from selection to the selection differential: $h^2 = R/S$. Dhanasobhon (6) further derived Falconer's formula for realized heritability

as the ratio of the difference between the mean values of the high ($\overline{X}_H$) and low ($\overline{X}_L$) selection-types in the generation of response (F_t) to the difference between the means of the selection-types in the generation selection is applied (F_{t-1}):

$$h^2 = \frac{\overline{X}_{H(F_t)} - \overline{X}_{L(F_t)}}{\overline{X}_{H(F_{t-1})} - \overline{X}_{L(F_{t-1})}} \; .$$

The mean values for high and low selection-types of kernels per spike were obtained for the F_3 progeny and their corresponding F_2 parent plants. Data for the F_2 were obtained from Larkins' (24) study. Applying the formula as described above, the realized heritability of kernels per spike was estimated to be:

$$\text{Population 1} \qquad h^2 = \frac{53.14 - 44.87}{55.73 - 32.52} = 0.356$$

$$\text{Population 2} \qquad h^2 = \frac{48.29 - 41.04}{54.77 - 31.20} = 0.308$$

These values are slightly higher than those reported by Dhanasobhon (6) and Sidwell (33), and indicate that early-generation selection would be useful in a breeding program.

Heritability estimates presented in Table VI resulted from the regression of each trait of the F_3 progeny on the corresponding trait of the F_2 parents in Populations 1 and 2. The estimate of heritability of yield was exaggerated due to the method of measurement. Yield was measured on the basis of a single plant in the F_2, whereas it was measured on a row basis averaged over three replications in the F_3. The estimates for yield presented in Table VI have been adjusted by the ratio of overall mean yield of the F_2 to that of the F_3 in each population. The adjusted heritability estimates for yield were 0.425 and 0.420 for Populations 1 and 2

respectively. The heritability estimate for kernels per spike was inter-
mediate in magnitude (0.341 in Population 1 and 0.295 in Population 2)
and highly significant in both populations. These estimates are in close
agreement with the realized heritability estimates previously mentioned.
They are higher than reported by Sidwell (33) but are in general agreement
with those of Paroda and Joshi (30). The heritability estimate for ker-
nel weight was not significant in either population. The heritability
value for yield was higher than those of the two yield components. This
differs somewhat from the reports of other workers (9, 17, 27, 30, 35).
Because of different units of measurement, the reliability of the adjust-
ed heritability estimate for yield is questionable. Plant height had a
heritability estimate which was high in magnitude and highly significant
in both populations (0.763 and 0.830 for Populations 1 and 2 respectively).

Genetic Correlations

Through a regression technique proposed by Hazel (16), genetic cor-
relations among grain yield, kernels per spike, kernel weight, and plant
height were calculated. Genetic correlations are shown on Table VII for
Populations 1 and 2. No test of significance was available for genetic
correlations derived through regression. However, some inferences may
be made by regarding the relative magnitudes of these correlations.

Grain yield was most highly correlated with kernels per spike, with
values of 0.580 and 0.955 for Populations 1 and 2 respectively. Sidwell
(33) reported a negative genetic correlation between grain yield and ker-
nels per spike. The results of this study are more in accordance with
Dhanasobhon (6) as to the sign; however, the magnitude of this correla-
tion in her study was much lower. Plant height had a correlation of

0.391 and 0.520 with yield in Populations 1 and 2, followed by kernel weight with a yield correlation of 0.253 in Population 1. The intermediate correlation between plant height and yield is in agreement with Johnson et al. (17). A low correlation between kernel weight and yield was also found by Sidwell (33).

The negative genetic correlations between kernel weight and kernels per spike of -0.274 and -0.562 for Populations 1 and 2 respectively, agree with those reported by Dhanasobhon (6). This was not manifest, however, in the present study by significant differences between high versus low selection-types in kernel weight. A low to intermediate, positive genetic correlation was seen in both populations (0.273 and 0.330, respectively) between kernels per spike and plant height. Sidwell (33) reported a highly negative genetic correlation between these two characters. The genetic correlation between kernel weight and plant height differs somewhat between the two populations. In Population 1 this correlation value was 0.214, lower in relation to Population 2 where it was 0.539. The correlation in Population 2 is more in line with Sidwell's (33) work.

<center>Grid Selection vs Selection Without Grids</center>

A standard analysis of variance was conducted on Larkins' (24) F_2 data to determine the within-grid (σ_W^2) and among-grid variance (σ_A^2) components of the total phenotypic variation (σ_T^2) in the F_2 where the ratio of the response from grid selection to the response to selection without grids $= \sqrt{\dfrac{\sigma_A^2}{\sigma_W^2} + 1}$.

The components of this formula and the efficiency of grid selection are presented in Table VII. The among-grid variance component estimate

was 0.85 and 0.15 for Populations 1 and 2, respectively. The within-grid variation was much greater with values of 109.17 in Population 1 and 116.41 in Population 2. Because the within-grid component of variation was so great in relation to the among-grid component, the ratio of response from grid selection to that from selection without grids was effectively 1:1. The estimated gain of efficiency in using grids for selection was only 0.4% in Population 1 and 0.1% in Population 2. These results are inconsistent with those of Verhalen et al. (37) using grid selection in cotton.

While selection for kernels per spike in this study was an effective means of indirect selection for yield, there was very little gain in efficiency through using grids. The space-planted nature of the F_2 populations combined with the fact that they covered only a small plot of land probably accounts for no gain in efficiency using grid selection.

CHAPTER V

SUMMARY AND CONCLUSIONS

Fifty-six F_3 progenies from each of two populations of winter wheat
were studied during the 1979-80 crop season. F 23-71, an unadapted Roman-
ian germplasm line which displays a high number of kernels per spike, was
used as the common parent for the two populations.. Caprock and TAM W-101
were used as the adapted parents in Populations 1 and 2, respectively.

Larkins (24) studied 256 F_2 plants from each of the two populations
described above. In his study, each population consisted of 16 grids,
each containing 16 bordered F_2 space plants. Based on measurements of
individual F_2 plants, a stratified grid method of selection for high and
low kernels per spike was used to obtain the material for this study.
Selections were made from 14 of the 16 grids.

The resulting F_3 progenies were planted in a split-plot design with
three replications. Each population consisted of 14 main plots, each of
which traced to a grid in Larkins' (24) study. Each main plot contained
four sub-plots which were progeny rows from the two high and two low se-
lections. Each sub-plot was evaluated for kernels per spike, kernel
weight, grain yield, plant height, and heading date.

Comparison of the high and low selection-type means for each trait
measured showed the F_3 responses to selection for kernels per spike in
the F_2. Differences between selection-types were highly significant for
the kernels per spike trait. Differences of 15.6% in Population 1 and

15.0% in Population 2 were observed. Differences between selection-types for yield were also highly significant. Differences of 24.7% and 28.6% were observed in Populations 1 and 2, respectively. Kernel weight remained relatively unchanged in both populations. These responses indicate that selection for kernels per spike was effective in increasing yield and are consistent with the findings of other studies concerning selection for kernels per spike (7, 13, 18, 27).

Realized heritability estimates for kernels per spike of 0.356 and 0.308 were observed in Populations 1 and 2, respectively. Heritability estimates for this trait from the regression of F_3 progeny on F_2 parents were 0.341 in Population 1 and 0.295 in Population 2. These values are slightly higher than those reported by Dhanasobhon (6) and Sidwell (33), and indicate that early generation selection for kernels per spike would be useful in a breeding program.

Genetic correlations between yield and kernels per spike, kernel weight, and plant height indicated that kernels per spike had the greatest effect on yield, followed by plant height and kernel weight in descending order. A negative correlation of low to intermediate magnitude was observed between kernels per spike and kernel weight.

An analysis of variance on the F_2 data showed that grid selection was no more effective than selection without grids would have been in this particular study.

The observed effects of selection for kernels per spike on grain yield, as well as heritability estimates for kernels per spike and genetic correlations indicate that selection for kernels per spike would be an effective method of indirect selection to improve grain yield.

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TABLE I

MEAN SQUARES FOR FIVE TRAITS FROM THE ANALYSES
OF VARIANCE OF POPULATION 1
(F 23-71/CAPROCK)

Source	df	Kernels/ Spike	Grain Yield	Kernel Weight	Plant Height	Heading Date
Main plot	13	65.94	858.65	49.85**	324.87*	32.33**
Seln-type (H vs L)	1	2,875.15**	28,644.76**	53.72	393.15	37.15
Main plot X Seln-type	13	47.01	2,309.80	22.02	155.57	45.11*
Sub-plot/Main plot, Seln-type	28	122.74**	1,703.43**	34.86**	277.67**	16.99**

*,**Significant at the 0.05 and 0.01 levels of probability, respectively.

TABLE II

MEAN SQUARES FOR FIVE TRAITS FROM THE ANALYSES OF VARIANCE OF POPULATION 2
(F 23-71/TAM W-101)

Source	df	Kernels/ Spike	Grain Yield	Kernel Weight	Plant Height	Heading Date
Main plot	13	79.99**	3,760.00**	70.34**	242.81**	10.45**
Seln-type (H vs L)	1	2,207.63**	53,407.27**	0.72	621.01	13.71
Main plot X Seln type	13	47.84	2,416.13	46.22	134.92	3.06
Sub-plot/Main plot, Seln-type	28	44.15*	2,926.61**	32.78**	221.94**	2.66**

*,**Significant at the 0.05 and 0.01 levels of probability, respectively.

TABLE III

MEAN RESPONSE OF FIVE TRAITS TO HIGH AND LOW SELECTION
FOR KERNELS PER SPIKE IN POPULATION 1
(F 23-71/CAPROCK)

Character Measured	Selection-type High	Low	Difference (High minus Low)	$\frac{H-L}{H}$ X 100 (Percent)
Kernels/spike	53.14	44.87	8.27**	15.60**
Grain Yield (g/plot)	105.79	79.67	26.12**	24.70**
Kernel Weight (g/1000)	31.07	32.20	-1.13	-3.60
Plant Height (cm)	102.20	99.14	3.06	3.00
Heading Date (days)[1]	41.60	40.66	0.94	2.30

[1]Days after March 31.

**Significant at the 0.01 level of probability.

TABLE IV

MEAN RESPONSE OF FIVE TRAITS TO HIGH AND LOW SELECTION
FOR KERNELS PER SPIKE IN POPULATION 2
(F 23-71/TAM W-101)

Character Measured	Selection-type		Difference (High minus Low)	$\dfrac{H-L}{H}$ X 100 (Percent)
	High	Low		
Kernels/spike	48.29	41.04	7.25**	15.00**
Grain Yield (g/plot)	124.78	89.12	35.66**	28.60**
Kernel Weight (g/1000)	34.74	34.87	-0.13	-0.40
Plant Height (cm)	106.58	102.74	3.84	3.60
Heading Date (days)[1]	41.93	42.50	-0.57	-1.40

[1]Days after March 31.

**Significant at the 0.01 level of probability.

TABLE V

MEANS OF FIVE TRAITS FOR THE TEN HIGHEST YIELDING ENTRIES,
PARENTS AND CHECKS OF POPULATIONS 1 AND 2

Entries	Selection-type	Kernels/spike	Grain Yield (g/plot)	Kernel Weight (g/1000)	Plant Height (cm)	Heading Date (days)[1]
Population 1 (F 23-71/Caprock)						
54003-7	H	51.7	146.6	34.3	108.7	42.0
54007-3	H	52.3	145.3	35.3	105.7	40.0
54008-2	L	56.3	136.7	33.0	108.7	39.3
54015-15	H	48.3	133.4	34.7	100.0	38.3
54007-4	H	46.3	132.3	34.0	102.0	38.3
54013-4	H	55.7	131.6	31.3	108.3	44.3
54016-16	H	57.0	125.1	32.0	101.0	38.0
54006-15	H	65.3	124.0	28.0	97.0	40.0
54018-7	H	56.3	123.0	31.3	107.0	40.0
54018-2	H	46.0	123.0	32.3	105.3	46.0
Population 1 Means		49.0	92.8	31.7	100.7	41.2
F 23-71	-	65.7	94.6	26.3	110.0	46.0
Caprock	-	44.3	88.3	26.3	81.7	40.3
Scout 66	-	41.7	120.2	29.0	107.3	42.0
Newton	-	50.3	92.5	22.3	88.3	42.3
Population 2 (F 23-71/TAM W-101)						
54021-16	H	49.0	173.9	36.3	110.7	41.0
54033-12	H	42.3	169.2	39.7	110.3	38.3
54035-4	H	39.0	167.4	39.7	113.7	41.3
54024-2	H	44.0	161.5	36.3	115.3	42.0
54033-11	H	46.7	159.5	41.0	110.7	39.3
54025-2	H	44.7	158.3	40.3	109.7	41.0
54021-8	H	46.7	156.2	35.3	117.0	41.0
54027-8	H	51.0	150.2	34.0	94.7	41.0
54037-8	H	47.3	146.4	33.3	111.3	42.3
54023-2	H	48.3	139.7	33.7	112.3	43.0
Population 2 Means		44.7	107.0	34.8	104.7	42.2
F 23-71	-	60.3	107.3	25.7	105.7	45.3
TAM W-101	-	37.7	103.7	33.0	84.0	41.0
Scout 66	-	39.3	125.7	30.0	109.7	41.7
Newton	-	52.0	84.3	23.0	89.3	42.3

[1]Days after March 31.

TABLE VI

HERITABILITY ESTIMATES FOR KERNELS PER SPIKE AND
THREE OTHER TRAITS OF POPULATIONS 1 AND 2

		Heritability Estimate	
Character	Method of Estimation	Population 1 (F 23-71/Caprock)	Population 2 (F 23-71/TAM W-101)
Kernels/spike	Realized h^{2}[1]	0.356	0.308
Kernels/spike	Regression	0.341**	0.295**
Grain Yield	Regression	0.425**	0.420**
Kernel Weight	Regression	0.179	0.148
Plant Height	Regression	0.763**	0.830**

[1]There was no available test for statistical significance of realized heritability estimates.

**Significant at the 0.01 level of probability.

TABLE VII

GENETIC CORRELATIONS BETWEEN FOUR TRAITS IN
POPULATIONS 1 AND 2

Character	Grain Yield	Kernel Weight	Plant Height
Kernels/spike	0.580	-0.274[1]	0.273
	0.955	-0.562	0.330
Grain Yield		0.253	0.391
		[2]	0.520
Kernel Weight			0.214
			0.539

[1]The upper values are the genetic correlations for Population 1 and the lower for Population 2.

[2]Corresponding regression coefficients differed in sign, therefore, Hazel's (16) regression technique was not applicable.

TABLE VIII

EFFICIENCY OF GRID SELECTION IN THE F_2 GENERATION FOR KERNELS
PER SPIKE IN POPULATIONS 1 AND 2

Components of Phenotypic Variance	Response to Grid Selection / Response to Selection Without Grids	Gain of Efficiency Using Grid Selection
Popn 1 (F 23-71/Caprock)		
$\hat{\sigma}_A^2$ (Among grid) = 0.85 $\quad$ $\hat{\sigma}_W^2$ (Within grid) = 109.17	$\sqrt{\dfrac{\hat{\sigma}_A^2}{\hat{\sigma}_W^2} + 1} = 1.004$	0.4 %
Pop 2 (F 23-71/TAM W-101)		
$\hat{\sigma}_A^2$ (Among grid) = 0.15 $\quad$ $\hat{\sigma}_W^2$ (Within grid) = 116.41	$\sqrt{\dfrac{\hat{\sigma}_A^2}{\hat{\sigma}_W^2} + 1} = 1.001$	0.1 %

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