

## AN ABSTRACT OF THE THESIS OF

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Title: Estimates of Genetic Variability and Efficiency of Early Generation Selection for Grain Yield and Protein Content in Durum Wheat Crosses (*Triticum turgidum*. L. var. *durum*).

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Dr. Warren E. Kronstad

Two of the major problems limiting the effectiveness of plant improvement are identifying the most promising parental combinations to hybridize and selecting superior genotypes in early segregating populations. Major factors contributing to these problems are the nature of inheritance and potential negative associations of the desired attributes. Objectives of the present study were to obtain information regarding the inheritance and degree of genetic association of selected agronomic traits including grain yield and protein content, and to evaluate responses to selection in F3 and F4 lines for these traits in durum wheat.

Combining ability estimates were obtained using four durum wheat cultivars of diverse origin crossed in diallel fashion. Data from parents, F1, F2, and F3 generations grown at two environmentally diverse sites over two years were examined using mean generation analysis. Effectiveness of single plant selection was evaluated using correlations between individual plant data from F2 and F3 and the same traits measured on F3 and F4 row progenies grown at the two locations. Unadjusted and adjusted F2 and F3 individual plant data were compared in

predicting row performance. Within cross heritability and responses to selection for kernel weight, grain yield, and protein content were estimated in F3 and F4 lines.

Combining ability analysis indicated that additive gene action is important in the inheritance of plant height, kernel weight, and protein content in this experimental material. Non-additive gene action played an important role in the inheritance of biomass, grain yield, harvest index, number of kernels per spike, and spike number. Based on  $g_i$  effects, the best parental cultivars would be 07690 Nic, Cak-Mak, and Parus for plant height, kernel weight, and protein content. The parental cultivars mean values were not good predictors of cross performance for biomass, grain yield, number of spikes, number of kernels per spike, and harvest index. Partial agreement between F1 mean values and  $s_{ij}$  effects were also noted for most traits except protein content. Results from mean generation analysis showed that environmental factors influenced both additive and dominance estimates. No significant genetic variability at the 5% level was noted for biomass, grain yield, number of spikes per plant in all crosses at both locations. Epistasis was involved in determining the inheritance of plant height, kernel weight, harvest index, and protein content.

Positive associations were obtained between grain yield and biomass, plant height, and kernel weight in both F3 and F4 lines. Dilution of a limited amount of protein content could be the cause of the negative association between protein content and grain yield. F2 and F3 single plant data for plant height, kernel weight, and protein content were associated with F3 and F4 row progeny performance. Estimates of heritability, progeny row predictions, and responses to selection indicated that early generation selection for kernel weight and protein content could be effective in improving both grain yield and protein content in these populations.

**Estimates of Genetic Variability and Efficiency of Early Generation Selection for Grain Yield and Protein Content in Durum Wheat Crosses (*Triticum turgidum*. L. var. durum).**

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Typed by REZGUI Salah

IN DEDICATION TO

my wife,

Sarra Amara

my son,

Youssef Rezgui

and my parents,

Amara and Rezgui

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# **Estimates of Genetic Variability and Efficiency of Early Generation Selection for Grain Yield and Protein Content in Durum Wheat Crosses (*Triticum turgidum*. L. var. durum)**

## **INTRODUCTION**

Breeders of self-pollinated crops are confronted by two major problems: a) identifying the best parental combinations that will result in the highest percentage of desirable progeny, and b) being effective in selecting in early generation. Creating genetic variability and identifying the most promising parental combinations is a difficult task due to the large amount of germplasm available. This is particularly true when attempting to improve quantitatively inherited traits such as grain yield where many genes are involved and a large environmental influence is present. Obtaining a sufficient quantity of F1 seed to evaluate imposes an additional constraint on the resources available to screen progenies of a large number crosses.

Biometrical models have provided an opportunity to determine the contribution of each parent to progeny performance and to ascertain the nature of gene action controlling quantitative traits. Application of such models can aid a breeder in choosing an appropriate strategy to be followed for plant improvement. Commonly used models include combining ability analysis and mean generation analysis. Combining ability analysis allows for the prediction of parental performance and partitions the components of genetic variation into additive and non-additive genetic effects. However, the reliability of these estimates remains in question, mainly because of the failure of the parental cultivars to satisfy the assumptions on which most of the analyses are based (Singh et al.1992). Two of these assumptions, the independent distribution of the genes and the absence of epistasis, are rarely, if ever, satisfied (Baker, 1978). Mean generation analysis provides valid estimates of additive genetic effects free from linkage bias provided that genotype x environment interactions are low (Ketata et al.1976). In addition, mean generation analysis provides estimates of the nature epistatic

effects involved in the inheritance of a particular trait.

There is a lack of agreement as to the value of early generation selection, particularly for quantitative traits such as grain yield (Weber, 1984; Mitchell et al. 1982). Lack of efficiency has been attributed to inadequate seed quantities, heterozygosity, spaced planting, and inadequate assessment of genotype x environment interactions (Wricke and Weber, 1986). Adjustment of single plant data to plot deviations in F<sub>2</sub> and F<sub>3</sub> segregating populations has been suggested as a way to improve predictions for grain yield of progenies grown in solid seeded conditions (Fasoulas, 1973; Knott, 1972; Mitchell et al. 1982; Hill et al. 1991).

Improvement of grain yield and protein content are major objectives of most durum wheat breeding programs. Several studies have indicated that simultaneous improvement of both grain yield and protein content are difficult to achieve due to the negative associations between these two traits. Source-sink relationships, environmental factors, and nitrogen translocation efficiency are the principal causes noted for the inverse relationship between grain yield and protein content in cereals (Kibite and Evans, 1984). O'Brien and Panozzo (1988) reported that genetic advances in both traits are possible in bread wheat when intensive selection for protein content is practiced in F<sub>2</sub> and F<sub>3</sub> generations prior to yield testing.

A diallel cross of four genetically diverse cultivars of durum wheat was used to 1) determine the nature of inheritance of grain yield, protein content, and selected agronomic traits using combining ability analysis and mean generations analysis, 2) assess possible associations between grain yield, protein content, and yield related traits in F<sub>3</sub> and F<sub>4</sub> lines, 3) study the use of unadjusted and adjusted single plant data in predicting the performance of row progenies from selected plants in the F<sub>2</sub> and F<sub>3</sub> generations, and 4) estimate responses to selection for kernel weight, grain yield, and protein content in F<sub>3</sub> and F<sub>4</sub> lines.

## LITERATURE REVIEW

### Genetic Diversity

Ethiopia is regarded as the center of origin of wild Emmer wheat, *Triticum turgidum* (L.) Thell.ssp. *dicoccoides* (Korn) Thell. Emmer, is the tetraploid progenitor of cultivated durum *Triticum turgidum* ssp. *turgidum* L. conv. *durum* (Desf). (Vavilov, 1951; Harlan, 1981). Durum wheat is currently cultivated in the Middle East, North Africa, Europe, the Soviet Union and the United States.

More than eight million hectares of durum are currently grown with improved durum cultivars derived from International Maize and Wheat Improvement Center (CIMMYT) germplasm (Singh et al.,1992). Concerns have been expressed that use of a limited genetic base could result in plateaus for grain yield and protein content, especially when crops are grown under unfavorable conditions. Also, genetic uniformity could introduce a greater risk of vulnerability to pests and diseases in more favorable environments (Porceddu et al. 1988; Blum et al.,1987). To avoid these potential problems, introducing favorable alleles from different gene pools into adapted germplasm is considered as successful strategy to enhance grain yield and other desirable agronomic traits (Srivastava et al. 1989).

Germplasm exchange exerts a major influence on the genetic constitution of cultivated durum wheats and accounts for a large proportion of the genetic variability observed in many breeding programs (Pecetti et al. 1992). Several studies (Jaradat, 1991; Hintum and Elings, 1991; Elings and Nachit, 1991) reported a close relationship between genetic variability and agro-ecological characteristics (day length, rainfall, temperature) suggesting that landraces are adapted to specific environmental conditions. However, Spagnoletti et al. (1985) attributed the

genetic diversity in landraces to limited selection for yield and its components. The germplasm introduced from diverse origins to the U.S.A and intensive breeding activities explained most of the variability found in this gene pool (Harlan, 1984). Over 7600 durum wheat accessions from 22 countries were assessed for their yield components, plant height, protein content, days to heading and maturity under semi-arid Mediterranean climatic conditions in Syria (Pecetti et al., 1992). On average, the greatest genetic diversity was observed in materials from India, Egypt, Ethiopia, Italy and the USA. North African gene pools were characterized by taller plants, higher protein content, and higher kernel weight. Germplasm from the USA, Turkey, Bulgaria, Afghanistan and France were characterized by tall stature coupled with high mean values for kernel number per spike and protein content.

### **Early Generation Selection Efficiency**

Individual plant selection in early segregating generations for grain yield and other agronomic traits has met with limited success. For highly inherited traits like kernel weight and plant height, early selection has proven successful in bread wheat (Islam et al.1985a; Quail et al. 1989). However, the response to early generation selection for quantitatively inherited traits including grain yield, has been limited. The most frequent reasons given for this failure in durum wheat include the inability to identify useable genetic variation and a large environment effect (Mitchell et al.1982).

However, investigators do not agree as to the value of prediction based on early generation performance, particularly for quantitatively inherited traits. Several authors have attributed the lack of phenotypic selection for grain yield based on single plants in F<sub>2</sub> segregating populations to environmental interactions and to the differential competition



between genotypes within populations (Sneep, 1977; McVetty and Evans, 1980). Wricke and Weber (1986) argued that the limited number of seeds available, spaced planting, and preponderance of dominance effects are the principal factors influencing the lack of efficiency of selection in F<sub>2</sub> or F<sub>3</sub> segregating populations; however, it was noted that delayed selection may seriously limit the genetic gain for quantitatively inherited traits such as grain yield (Sneep, 1977). This is due to the decrease of frequency of high yielding genotypes in advanced generations. Valentine (1979), working with barley, suggested that no opportunity for selection for grain yield in the earlier generation should be lost. He pointed out that selection for grain yield between families on a plot basis in F<sub>3</sub> and subsequent generations was more efficient than between individual plants in the F<sub>2</sub> generation. Nevertheless, he indicated some genetic advance in grain yield can be achieved by selecting for plant height, kernel number, kernel weight among spaced plants in the F<sub>2</sub> generation.

Evidence of environmental influence, interplant competition, and compensation effects of yield components has been reported by several authors in wheat (Gebre-Mariam et al. 1988; McVetty and Evans, 1980). Royo and Ramagosa (1988) studied different genotypes of bread and durum wheat cultivars sown at different population densities and under variable climatic condition. They found that harvest index and kernel weight were the most reliable predictors of grain yield for bread wheat; however, no selection criteria involving any of these traits was found to be suitable for durum wheat. Bhatt (1980) pointed out that selection for yield components on spaced plants in wheat can not be generalized for all growing conditions because of unpredictable environmental changes. Fasoulas (1973) attempting to improve response to selection for grain yield in wheat, proposed adjustment of individual F<sub>2</sub> plant data to neighboring plants. Later, Mitchell et al. (1982) found that selection response for grain yield in F<sub>2</sub> segregating populations of durum wheat by using 60 cm spacing between plants in

F2 populations was superior to Fasoulas's approach. They concluded that opportunity exists to select for grain yield under spaced-planted conditions that were conducive to higher single plant yield and greater range of variability for this trait. Recently, Hill et al. (1991), argued that F3 row performances can be predicted from F2 data in oats using adjusted single plant data. However, they found that unadjusted plant observation was more reliable to predict F3 rows particularly for highly inherited traits such as plant height.

Results from these studies suggest that the nature of gene action controlling the expression of a trait and associations between selection criteria are important elements to consider in early generation testing for yield and protein content. Most of the results ascribed the observed genetic variability to additive gene action where a high frequency of transgressive segregation was obtained for the components of yield and protein content. However, both additive and dominance types of gene action were found to control the expression of grain yield. The following review will cover pertinent literature regarding estimates of gene action, associations, and the reliability of early generations selection for yield, yield components, harvest index and protein content.

## **Grain Yield**

Genetic diversity among parents is considered essential for long-term improvement of grain yield in durum wheat. Abundant genetic variation for grain yield was found to occur among crosses between parental cultivars from different gene pools in durum wheat (Spagnoletti et al., 1985; De Pace et al., 1985).

Investigations on the nature of gene action for grain yield in durum, as ascertained through a diallel cross, suggest that general combining ability accounts for the majority of the

total genotypic variance among crosses (Quick, 1978). However, estimates of general and specific combining abilities observed in these studies were not consistent. Such inconsistencies might be attributed to the different parents included in the analyses and a bias due to the interaction between general combining ability and the environment (De Pace et al. 1985). Using mean generation analysis in four crosses of durum wheat, Amaya et al. (1972) reported that dominance effects were relatively more important than additive effects in the inheritance of grain yield. However, Gill et al.(1983) reported that additive and dominance effects are equally involved in the expression of grain yield.

The number of genes involved, low heritability, and the large genotype by environment interaction rendered selection for grain yield per se in early segregating generations difficult to achieve in durum (Cantrell and Haro-Arias, 1986). In bread wheat, Islam et al.(1985a, 1985b) reported that selection for grain yield on both a per plant basis in F<sub>2</sub> populations and on a per line basis in solid seeded F<sub>3</sub> generations were both ineffective as compared to selection for components of yield in bread wheat. They concluded that components of yield are more heritable and more stable than grain yield itself (Islam et al.1985a). Because of this, selection criteria such as number of spikes, number of kernels per spike, kernel weight, plant height, and harvest index have used in early generation selection to enhance grain yield in durum wheat (Mitchell et al. 1982; Pecetti et al.1992 Royo and Romagosa 1988).

### **Number of Spikes per Plant**

Genetic variation for spike number per plant is available in durum wheat (Spagnoletti et al. 1985); however, non-additive gene action largely governs the expression of this trait (Quick 1978; Bhattia et al. 1979; Spagnoletti et al. 1985). Narrow sense heritability estimates of 0.13 for spike number were reported by De Pace et al. (1985) in a diallel cross involving six parents. The low to intermediate estimates of heritability reported in the literature for this trait are higher than those associated with grain yield. Nevertheless, these estimates were lower than those estimated for number of kernels per spike and kernel weight (De Pace et al. 1985).

Bakheit et al. (1989), studied the associations between several traits in parents, F1 and F2 generations involving eight parental cultivars of durum wheat under normal field and aphid infestation conditions. They found consistent and positive genotypic correlations between number of spikes and plant height, grain yield, and biomass. Negative associations were found between number of spikes and harvest index, and thousand kernel weight. In addition, number of spikes per unit area was significantly and negatively associated with kernel weight and kernel number per spike suggesting the existence of compensation effect among these traits (Cantrell and Haro-Arias, 1986; Quick, 1978). Although, spike number was found to have the largest direct effect on grain yield, environmental factors exerted an important effect on the expression of this trait (Joppa and Williams, 1988). Competition for nutrients, water, and light among progenies in segregating populations often result in a limited response to selection in earlier segregating generations. McNeal et al (1978) found low response to selection for number of spikes per plant in F8 lines of bread wheat. They concluded that this trait is not an effective selection criterion to enhance grain yield.

### Number of Kernels per Spike

Specific combining ability accounted for 76% of the genetic variation observed in number of kernels from a diallel cross involving six parents of durum wheat (De Pace et al., 1985). However, Spagnoletti et al. (1985) reported that general combining ability was as important as specific combining ability in a diallel cross of ten cultivars. Other studies, found that kernel number is controlled mainly by additive gene action (Bhattia et al. 1979). Using parent-offspring regression, De Pace et al. (1985) found a low narrow sense heritability estimate of 0.01 computed from the components of variance.

The higher yield of semi-dwarf durum cultivars is attributed to a higher spikelet fertility leading to increased kernel number per spike (Ledendt and Moss, 1979). Using *Tetrastichon* or four row spike (FRS) to increase the number of kernels, Haugerud and Cantrell (1984) did not detect a significant difference between the FRS lines and standard cultivars in durum wheats. Although this trait was found to be positively associated with grain yield, Haugerud and Cantrell (1984) noted that increased kernels per spike had a detrimental effect on kernel weight and attributed the limited response in grain yield to compensation between components of yield.

Single plant selection in F<sub>2</sub> populations from two crosses of bread wheat increased grain number per spikelet and grain yield per plant (Islam et al. 1985a). Similar results were found by selecting for number of kernels per spike in F<sub>3</sub> lines from two crosses of bread wheat grown under low and high planting densities (Islam et al., 1985a).

## **Kernel Weight**

In durum wheat, thousand kernel weight ranges from 20 to 60 g. Low kernel weight tends to reduce milling extraction percentage and semolina yield (Joppa and Williams, 1988).

Kernel weight is controlled largely by additive gene action (Spagnoletti et al., 1985). A broad sense heritability estimate of 0.86 was observed in two populations (Haugeraud and Cantrell, 1984), while narrow sense heritability of 0.58 was computed from 45 crosses (De Pace et al., 1985). This trait was found to be an important predictor of grain yield in bread wheat but not in durum wheat (Royo and Romagosa, 1988).

Several investigations have indicated that kernel weight is the most important component of grain yield due to its high positive association with grain yield (Quick, 1978; Haugerud and Cantrell, 1984). However, the merit of kernel weight as a selection criterion appears to depend on the effect of environment during grain filling and to its association (most often negative) with the number of spikes per plant and spikelet fertility (Joppa and Williams, 1988). Pinthus (1987) pointed out that no particular kernel size was associated with grain yield when evaluated in F5 lines from four crosses of bread wheat, whereas, McNeal et al. (1978) obtained a gain of 2.8 g from early generation selection for kernel weight in bread wheat. Islam et al. (1985a) also found a low correlated response in grain yield by selecting for kernel weight in F2 segregating populations of bread wheat. Quail et al. (1989) reported a negative association between kernel weight in the F3 generation and grain yield in the F7 and the F8 in bread wheat.

## **Plant Height**

Under favorable growing conditions, durum wheat cultivars range from 96 cm to 165 cm in height. Short cultivars are found in semi-arid areas; whereas, taller cultivars are found in countries with late spring rainfall and relatively colder winters ( Pecetti et al.,1992; Jaradat, 1991).

Plant height is highly heritable and less affected by the environment than other traits. This trait is considered one of the most useful criteria for selection for yield potential in early generation because reduced height often predicts increased yield (Whan et al.1982). Quail et al.(1989) found that increased grain yield was associated with reduced plant height in bread wheat. A narrow sense heritability estimate of 0.72 was reported by De Pace et al. (1985) suggesting that the expression of plant height is controlled by additive effects. General combining ability was predominant in the expression of plant height in a diallel analysis in durum wheat (Spagnoletti et al. 1985; De Pace et al., 1985).

Studies of associations between plant height and grain yield and yield components have produced mixed results. Small but positive associations between plant height and kernel per spike, kernel weight and grain yield were computed from a collection of 868 genotypes of durum wheat from Jordan (Jaradat, 1991). Nevertheless, Bakheit et al.(1989) found that plant height was positively associated with biological yield and number of spikes per plant but was negatively associated with kernel weight and harvest index in diallel crosses of eight durum cultivars. The association between plant height and grain yield, however, was inconsistent over generations. Comparing near-isogenic semi-dwarf and tall lines of durum wheat, Joppa (1973) reported that semi-dwarf durum wheats are characterized by a greater tillering capacity but lower test weights than taller types.

## Harvest Index

Harvest index (the ratio of grain yield to total above ground biomass) represents the relative ability of the plant to partition metabolites into grain yield (Donald, 1962).

Assessment of breeding on grain yield improvement over an extended period suggested that translocation of assimilates into the grain is more efficient in modern cultivars. Nevertheless, the production of total dry matter per unit area (biological yield) has not been affected by breeding activities in cereals (Feil, 1992). Evaluating representative cultivars of durum and bread wheats released in India during the past 80 years, Kulshrestha and Jain (1982) observed that most of the cultivars produced similar biomass. They attributed the improvement of yielding ability in the modern cultivars almost exclusively to selection for higher harvest index and increased kernel number. Perry and D'Antuono (1989) reported a slight increase of biomass when comparing old and modern Australian cultivars. They observed that cultivars with a semi-dwarf background were equal in biomass but had higher grain yield, harvest index, spike per unit area and number of kernels per spike than tall cultivars. They concluded that the increased yield potential had been achieved through substantial increases in kernel number per area coupled with shift in harvest index.

Several investigators have reported that general combining ability is greater than specific combining ability effects in controlling the expression of harvest index in bread wheat (Nass and Jui, 1985; Nanda et al., 1983) and in durum wheat (Srivastava et al., 1985). This suggests that additive gene action is predominant in the expression of this trait. Inconsistent general and specific combining ability estimates were found among progenies of a diallel cross involving seven diverse bread wheat parents in three environments (Sharma et al. 1991). They obtained narrow sense heritability estimates ranging from 0.44 to 0.60.



Some studies have suggested harvest index as a useful selection criterion, especially in a spaced plant conditions in bread wheat (Nass, 1980; Ellison et al., 1985; Donald and Hamblin, 1976). Others have found it to be of little value when determined on materials grown in a competitive situation (McVetty and Evans, 1980; Whan et al. 1982; Sharma and Smith, 1986). The use of parents having higher biomass or higher harvest indices in a breeding program to increase grain yield in bread wheat was proposed by Donald and Hamblin (1976). They indicated that the positive association between harvest index and agronomic characters would result in higher grain yield, early maturity and shorter genotypes. Sharma and Smith (1986) found that harvest index measured in the F3 generation was a good predictor of this trait in the F4, but not of grain yield in three bread wheat populations. Quail et al.(1989) did not find increased grain yield in F7 and F8 generations by selecting for harvest index in F3 generations in bread wheat.

Royo and Romagosa (1988) assessed yield components and harvest index on spaced plants as indirect selection criteria for grain yield under commercial densities in bread and durum wheats. They reported that harvest index and thousand kernel weight were the most stable selection criteria for improving grain yield in bread wheat. No consistent association between these traits measured on a per plant basis and grain yield measured on a per plot basis in durum wheat was detected. Damisch and Anneliese (1991) showed that biomass has to reach a certain level prior to flowering in order to benefit both grain yield and harvest index. Bakheit et al. (1989) reported positive and significant genotypic associations between harvest index, grain yield, and thousand kernel weight in both F1 and F2 generations from a diallel cross of eight durum cultivars.

## Protein Content

The kernels of durum wheat contain storage proteins that are essential for end use quality of food products such as breads, spaghetti, couscous and other pastas (Joppa and Cantrell, 1990). Evaluation of a large of durum wheat germplasm collection representing different gene pools showed a range in protein content from 7 to 22 % (Pecetti et al., 1992; Negassa, 1986). According to Harlan (1981), Emmer wheat accounts for most of the genetic variability of grain protein percentage in cultivated durum wheats. Several authors attributed the genetic variability in grain protein in durum and bread wheats to a differential translocation efficiency of nitrogen compounds among cultivars (Kushnir and Halloran, 1984; Levy and Feldman, 1987; Cox et al. 1985a; 1985b; Paccaud et al. 1985).

Lelly (1976) reviewed the literature on the inheritance of protein content and grain yield in wheat. He concluded that 1) much genetic variation exists for grain yield and protein content, 2) the inheritance of these two traits is complex, and 3) the heritabilities of both are high enough to expect progress through selection. Several investigations reported a negative association between protein content and grain yield in bread wheat (Cox et al., 1985a, 1985b; Noaman et al., 1990) and in durum wheat (Zitelli et al., 1978). Kibite and Evans (1984) attributed the negative association of these two traits to 1) environmental factors, 2) source-sink relationship, and 3) the dilution of protein by non-protein compounds.

There are conflicting reports concerning the effect of plant height, harvest index, and biomass on protein content. Several workers have reported that increased grain yield and harvest index in semi-dwarf cultivars of durum are associated with a reduction in protein content (Gale, 1979; Gale et al., 1981). Anna et al. (1986) showed that tall lines had consistently higher test weight, kernel weight and grain protein but lower grain yield than

semi-dwarf lines in four crosses of durum wheat. They concluded that an increased number of kernels was responsible for the lower protein content in semi-dwarf lines.

Sarrafi et al. (1989) noted that additive gene action controlled the expression of protein content. They reported a narrow sense heritability estimate of 0.78 in reciprocal crosses between six durum cultivars. Lapoujade et al.(1991) reported intermediate estimates of broad and narrow sense heritability for protein content ranging from 0.38 to 0.68 in a cross between an Ethiopian line (Ensaf-508) and a French cultivar (Opale) . Other authors reported heritability estimates ranging from 0.38 to 0.74 in durum wheat (Avivi et al.1983; Vallega 1985), suggesting that early generation selection should be moderately successful. In bread wheat, Johnson et al. (1985) reported that much variation for protein content was independent of grain yield and simultaneous advances would be possible. Thus, using intensive selection for protein content in early generations (F<sub>2</sub> and F<sub>3</sub>) prior to yield testing has proven effective in increasing both traits in four crosses of bread wheat (O'Brien and Panozza, 1988). Response to selection for protein content in the F<sub>3</sub> generation of six crosses of bread wheat ranged from 0.5 to 1.1 % when the selections were grown in F<sub>4</sub> yield trials (Guthrie et al.1984). Legge et al.(1991) evaluated the effectiveness of selection for protein content in F<sub>5</sub>'s grown in replicated hill plots from selections made in F<sub>2</sub> and F<sub>3</sub> generations of six durum crosses and found that response to selection ranged from 0 to 0.4% in protein content. They attributed the low responses to genotype x environment interactions resulting from contrasting and unfavorable conditions during the grain filling period. They concluded that response to selection in F<sub>2</sub> and F<sub>3</sub> is too low to justify the effort to select for protein content in early generations.

## MATERIAL AND METHODS

### Study 1

Four durum wheat genotypes (*Triticum turgidum* L. var. durum) representing a wide range in genetic diversity for plant type, maturity, grain yield, and protein content, were selected for this investigation. The parents were: Wd-Neb 021, Cak-Mak 79, Parus, and 07690 Nic. A more detailed description of these parents is provided in Appendix, Table 1.

### Experiment 1

A four-parent diallel cross excluding reciprocals was developed during the spring of 1989 at the Hyslop Crop Science Field Laboratory located 10 km northeast of Corvallis, Oregon. The four parents along with the six F1 populations were sown on October 25 1989 at East Farm located 1.16 km east of Corvallis. The soil type at this site is a Chehalis fine-silty, mixed, mesic, cumulic, ultic, Haploxeroll. A randomized complete block design with three replications was used. Plots consisted of 2 rows per entry. Rows were 3.6 m long and 0.3 m apart. Plants were spaced 0.3 m within a row allowing a total of 13 plants per row. Barley was sown around the perimeter of the experiment to avoid border effects. Prior to seeding, 70 kg ha<sup>-1</sup> of nitrogen as ammonium nitrate (34-0-0) was applied to the experimental area. Two additional applications of 45 kg ha<sup>-1</sup> were broadcasted at growth stages 18 and 50 of Zadoks' scale (Zadok et al. 1974). Finesse (Chlorosulfuron) was applied at a rate of 18 g ha<sup>-1</sup> at growth stage 31 of Zadoks' scale. Handweeding was performed at both 24 and 60 growth stages of Zadoks' scale. The fungicide Tilt (Propiconazole) was applied at the rate of

0.22 t ha<sup>-1</sup> at 32 and 49 growth stages of Zadoks' scale to control fungal diseases. At maturity, seven plants were selected in the middle of each row and data were recorded on a per plant basis for the following traits:

- 1) Plant height: measured as the distance in centimeters between the base of the culm and the tip of the main tiller excluding awns.
- 2) Spike number: number of fertile spikes at harvest.
- 3) Biomass: total weight in grams of plant cut at ground level.
- 4) Grain yield: total grain weight of the harvested spikes in grams.
- 5) Harvest index: calculated as the ratio expressed in percent of grain yield over biomass (grain yield/biomass) x 100.
- 6) Kernel weight: weight in grams of 200 randomly selected kernels.
- 7) Number of kernels per spike : average number of kernels determined from three randomly selected spikes.
- 8) Protein content: A 10 to 12 g sample from each plant representing parents and F1 generations (F2 seeds) were ground in a Udy cyclone mill using 0.5 mm mesh sieve. Grain protein content of the wholemeal flour produced was determined by near infrared reflectance spectroscopy using a Technicon InfraAlyzer 400 that was calibrated using samples of known protein content determined by Kjeldhal nitrogen method.

An analysis of variance was carried out to test for significant differences among entries. General combining ability and specific combining ability for parents and F1 's were estimated following method 2, model 1 (fixed effects for genotypes) of Griffing (1956) for all traits. The fixed model was applied because the parental cultivars were chosen and therefore inferences will be restricted to these parents .

## Experiment 2

The experimental material consisted of parents, F1's that were obtained by crossing the four cultivars during the summer 1989, F2 populations that were derived from the previous experiment at East Farm. The F3 populations were developed as follows. Seed from F1 crosses made in 1989 along with the parents were grown during Summer 1989 in the green house following vernalization for 40 days at 4°C in a growth chamber with a 12 hour photoperiod. A diallel cross involving the five parents was carried out to develop F1 populations for next season. Five seeds from each F1 hybrid were advanced to provide F2 seed. At maturity 100 F2 seeds from each cross were grown to develop F3 populations. At maturity, the F2 populations were bulked and a random sample of 200 grams was extracted. The parents, F1, F2, and F3 populations were sown in October 1990 in a randomized complete block design with three replications at Ruggs experimental site located 6 km east of Adams, Oregon. The soil type at this site is a coarse silty typical Haploxeroll. Plots consisted of two rows for F1s and parents and seven rows for F2 and F3 populations. A total of 13 plants were sown in each row of 3 m length. Spacing of plants was 0.3 m within and between rows. Prior to sowing, the experimental area was pre-irrigated with 200 mm of water. Ammonium sulfate (21-0-0) was broadcast at a rate of 70 kg ha<sup>-1</sup> before sowing and an additional application of 50 kg ha<sup>-1</sup> was broadcast at growth stage 18 of Zadoks' scale. Harmony Extra (Thiophensulfuron-methyl) at a rate of 30 g ha<sup>-1</sup> and Buctril (Bromoxynil) at a rate of 6 l ha<sup>-1</sup> were applied at growth stage 29 of Zadoks' scale. Bayleton (Triadimefon) at a rate of 500 g ha<sup>-1</sup> was applied at growth stage 47 of Zadoks' scale to protect the material against stripe rust (*Puccinia striiformis*). At maturity, 10 plants from the middle of each row were tagged and measurements were taken on a per plant basis. Due to missing plants in

some rows and low performances and shrivelled kernels due to heavy rust, records were standardized on seven plants per row. Data were collected and analyzed for plant height, biomass, grain yield, harvest index, 200 kernel weight, and protein content as described in the previous study.

Weighted least square of the generations mean analysis within each cross was used to determine the nature of gene action (Mather and Jinks 1982). The parameters fitted by weighted least squares were  $m$  (mean of all generations),  $a$  (pooled additive effects), and  $d$  (pooled dominance effects). The genetic assumptions were: 1) homozygous parents, 2) absence of linkage, 3) absence of lethal gene combinations, and 4) constant viability for all genotypes. Since durum wheat is autogamous, assumptions 1, 3, and 4 are reasonable. Parents are highly inbred and consequently most lethal gene combinations would already have been exposed and eliminated. Bias due to linkage is possible due to its effect on the random assortment of genes however, it is probably of more importance when epistasis is present (Mather and Jinks, 1982). A joint scaling test using information from the five generations was calculated to detect possible allelic interactions. Separate scaling tests for epistasis  $axa$  (pooled effects of additive by additive) and  $dxd$  (pooled effects of dominance by dominance) were carried out using the following scales respectively.

$$\begin{aligned}\overline{C} &= 4 \overline{F_2} - 2 \overline{F_1} - \overline{P_1} - \overline{P_2} \\ \overline{D} &= 4 \overline{F_3} - 2 \overline{F_2} - \overline{P_1} - \overline{P_2}\end{aligned}$$

These tests should be equal to zero within the limit of their respective standard errors. When a three parameters model was not sufficient to explain the genetic variability, a five parameters model was fitted according to Hayman (1958) to estimate the different genetic effects. Genetic effects were tested against their standard errors obtained from the variance of the corresponding population means.

### Experiment 3

The two parents, F1, F2 and F3 generations from each of the six crosses were sown at East Farm on October 17, 1991. A randomized complete block design with three replications was used. Each plot consisted of one row for each F1 and parents and five rows each for F2 and F3 populations. Each row was 4.5 m long and spacing was 0.3 m between and within rows allowing a total of 15 plants per row. Ammonium nitrate sulfate (16-20-0) was applied before sowing at a rate 150 kg ha<sup>-1</sup>. Ammonium sulfate (21-0-0) was applied at the same rate and broadcast as a top dressing at 22 growth stage of Zadoks' scale. Finesse (Chlorosulfuron), a herbicide, was applied at a rate of 18 g ha<sup>-1</sup> at 32 growth stage of Zadoks' scale. Plots were protected against leaf diseases using Tilt (Propiconazole) at a rate of 0.22 l ha<sup>-1</sup> applied at 47 growth stage of Zadoks' scale. Measurements were taken on per plant basis for plant height, number of spikes per plant, biomass, grain yield, 200 kernel weight, and protein content as previously described. Mean generation analysis (Mather and Jinks, 1982) was used to obtain estimates of gene action as described in Experiment 2.



## Study 2

This study was established to evaluate possible associations of selected agronomic traits between single plant selection under spaced planted conditions and solid seeded conditions. The principal objective was to test early generation selection criteria. Emphasis was given to examining associations between traits measured on individual F2 and F3 plants (from experiment 2 grown at the Ruggs site, 1991) with the same traits measured on progeny rows F3 and F4 grown under solid seed conditions. The row progenies were evaluated at two locations the following growing season 1992. The selection criteria considered in this study included plant height, kernel weight, protein content, biomass, grain yield and harvest index. Twenty F2 and twenty F3 individual plants from each of the six crosses grown at the Ruggs site during the previous growing season (Study 1, Experiment 2) were selected. Each selected plant was given a code so that single row progeny could be traced back to an individual plant. Data collection for individual plants, management practices, and spacing between segregating populations were those described in Study 1, Experiment 2. A random sample of 600 seed from each selected plant was required to establish F3 and F4 row progenies grown in three replications at the East Farm and Ruggs sites during the 1991/92 growing season. The climate, soil type information, and management practices were the same as described in the first study. Each row plot was 1.10 m in length representing a single F3 or F4 line. Rows were placed at 0.25 m apart. The seeding rate was 80 and 90 seed within a row representing the commercial seeding rates at Ruggs and East Farm sites, respectively. Sowing dates were October 17 and October 31, 1991 at Ruggs and East Farm, respectively. Jackmar, a club wheat cultivar was planted around the experimental area to avoid border effects. Material was sown in a split block design with three replications at both experimental sites. A replication

comprised six blocks and each block represented a cross with F3 or F4 lines as subplots. The experiment was analyzed as a nested block arrangement (lines nested within crosses) for each of the F3 and F4 generation. Data were collected on a per row basis for the following traits:

- Plant height: (cm) measured from the ground to the tip of the plants excluding awns (average of three observations taken at both edges and the middle of each row).
- Biomass: (g) weight of the bundle of the row cut at the ground level.
- Grain yield (g) weight of the total grains harvested from each row plot.
- Harvest index (%) calculated as the ratio of grain yield to above ground biomass.
- 200 kernel weight: (g) weight of a random sample of 200 kernels from each row plot.
- Protein content in (%). 10 g from each row plot were ground in a Udy cyclone mill using 0.5mm mesh sieve. The wholemeal flour produced was used to determine the grain protein by near infrared reflectance spectroscopy using a Technicon InfraAlyzer 400 that was calibrated by samples of known protein content determined by Kjeldahl nitrogen method.

Two methods of prediction for F3 and F4 row performance from individual F2 and F3 plant data were employed. Following the notation proposed by Hill et al. (1991) these two methods are:

1) Individual F2 or F3 plant performance (Model I),

where:  $y_{F3}=y_{F2}$  and  $y_{F4}=y_{F3}$  and where  $y_{F2}$  and  $y_{F3}$  are the observed values of the individual F2 or F3 parent of the F3 or F4 rows respectively.

2) Parental means plus unweighted F2 or F3 plot deviations, (Model II),

where:  $y_{F3} = 1/2(\bar{y}_{Pg} + \bar{y}_{Ph}) + 1/2(y_{ghijF2} - y_{ghi.F2})$

and  $y_{F4} = 1/2(\bar{y}_{Pg} + \bar{y}_{Ph}) + 1/2(y_{ghijF3} - y_{ghi.F3})$ , and where  $\bar{y}_p$  and  $\bar{y}_{ph}$  are the means of parent g and parent h respectively from F2 and F3 experiment,  $y_{ghijF2}$  and  $y_{ghijF3}$  the observed value of the plant j from the cross between parents g and h in replication i of the

previous experiment.  $y_{ghi.F2}$  and  $y_{ghi.F3}$  are the means of the plots in which the plant appeared.

The adjustment of individual plant values to deviations from the plot mean was done to remove replication effects in the previous experiment (Hill et al. 1991).

Genotypic correlations between traits were computed as:

$r_g = \sigma_{gx,y} / (\sigma_{gx}^2 \sigma_{gy}^2)^{0.5}$ , where  $\sigma_{gx,y}$ ,  $\sigma_{gx}^2$ , and  $\sigma_{gy}^2$  were estimates of genetic covariances and variances respectively from analysis of variance and covariance for each of these traits.

Expected response to selection for kernel weight, grain yield, and protein content were estimated within cross as:  $R = kh\sigma_{gx}$  where  $k=1.4$  is the coefficient at 20% selection intensity.

The correlated responses for each pair of traits were computed as:  $CR = kh_x\sigma_{gx}r_{g(x,y)}$ , where  $h_{(x)}$  is the square root of heritability estimates of the directly selected trait  $x$ ;  $\sigma_{gy}$  is the genotypic standard deviation for the indirectly selected trait  $y$ ; and  $r_{g(x,y)}$  is the genotypic correlation between  $x$  and  $y$  traits (Falconer, 1981).

## **RESULTS AND DISCUSSION**

### **Study 1. Genetic Variability Resulting from a Diallel of Genetically Diverse Parents of Durum Wheat**

#### **General Combining Ability Analysis**

It is important to the plant breeder that acceptable levels of genetic variability exist with breeding populations. Furthermore for the breeder of self pollinating species, like durum wheat, only that portion of the total genetic variability which responds in an additive manner can be exploited. One way of determining the nature of gene action influencing a trait is through the use of combining ability estimates. More specifically, it is general combining ability (GCA) which is of most interest as it estimates the amount of additive genetic variation present. Observed mean squares for entries, general and specific combining ability estimates, and their ratios for the eight traits studied are presented in Table 1. Significant genotypic variation was present among the ten entries (parents and F1's progenies) for the eight traits studied. Therefore, a partitioning of the observed genetic variability into general versus specific combining ability for each trait was justified. Highly significant differences were observed for (GCA) for all traits, except harvest index where the GCA estimate was significant at the 5% level. Specific combining ability (SCA) mean squares were highly significant for all traits other than protein content which was significant at the 5% level. These results indicated that both GCA and SCA were important in the inheritance of all traits studied.

In a diallel analysis, GCA is a function of additive genetic effects. Although estimates of GCA may involve some dominance effects when parents are included in the analysis (Singh and Paroda, 1984), the relative magnitude of additive versus non-additive variances for the various traits can be revealed by the GCA/SCA ratios. These ratios were greater than unity for plant height, kernel weight, and protein content. A ratio equal to unity for spike number, and less than unity for biomass, grain yield, harvest index and kernel number was observed. Since GCA provides an estimate of additive gene action while SCA provides an estimate for non additive gene action, GCA/SCA ratios suggested that the total genetic variability among the F1's for plant height, kernel weight, and protein content, was mainly due to additive gene effects existing among the parents. However, additive and non-additive effects were equally important in the inheritance of number of spikes. Non-additive gene effects exerted a greater influence on the expression of biomass, grain yield, harvest index, and kernel number.

A comparison of these results with other investigations indicated only a partial agreement regarding the nature of gene action involved in the inheritance of the same traits. Quick (1978) using 55 crosses obtained from 11 durum cultivars evaluated in a solid seeded experiment reported that yield, yield components, and plant height were mainly controlled by additive effects. However, number of spikes and number of kernels per spike were found to be inherited in non additive fashion in other studies involving different durum cultivars (Spagnoletti et al. 1985, Bhattia et al. 1979). Kernel weight, plant height and protein content were controlled mainly by additive gene action in several diallel crosses of durum (De Pace et al. 1985, Spagnoletti et al. 1985, Zitelli et al. 1978). Greater importance of GCA for harvest index, biomass and grain yield in durum was found by Srivastava et al. (1985).

The disparities between the results of this experiment regarding the nature of gene action involved in the expression of grain yield, biomass, and harvest index with those

reported earlier may arise from several sources: the number of parents selected, the genetic diversity present in the parental cultivars, and genotype x environment interactions. More than four, closely related, parental cultivars were usually evaluated in previous studies. In this study four distantly parental cultivars were used. The four parental cultivars belong to different gene pools ranging from winter (Wd-Neb 021 and Parus), facultative winter (Cak-Mak) and spring types (07690 Nic). Thus, it is expected to have a larger heterogeneity of variances of each array (parents and F1). Finally, the genotype by environment interactions and the precision of the experiment could have contributed to these differences.

The present GCA/SCA relationship would encourage early generation selection for plant height, kernel weight, and protein content since the additive gene effects which were prominent for these traits, are retained. If these estimates of gene action are unbiased, plant height and kernel weight could be used as selection criteria to improve grain yield provided that compensatory effects between these traits and other yield components are low. However, grain yield enhancement using these traits would depend as well on the nature of association between these traits and grain yield. In durum wheat, Quick (1978) found positive correlations between plant height, kernel weight and grain yield. In contrast, other workers reported that kernel weight may not enhance grain yield due to the negative association of this trait with number of kernels per spike (Haugerud and Cantrell, 1984), and number of spikes per plant (Joppa and Williams, 1988; De Pace et al. 1985).

Table 1. Observed mean squares for general combining ability (GCA) and specific combining ability (SCA) for : plant height (HT), spike number (SP), biomass (BM), grain yield (GY), harvest index (HI), kernel number (KN), kernel weight (KW), and protein content (P) from a 4x4 diallel cross grown at East Farm in 1989-90 growing season.

Source	d.f.	HT (cm)	SP	BM (g)	GY (g)	HI(%)	KN	KW(g)	P(%)
Replication	2	12.36	1.72	30.10	24.62	10.95	217.33	0.0002	0.18
Entries	9	203.46 <sup>***</sup>	29.14 <sup>***</sup>	2051.63 <sup>***</sup>	297.26 <sup>***</sup>	13.31 <sup>*</sup>	143.87 <sup>***</sup>	3.63 <sup>***</sup>	2.41 <sup>***</sup>
GCA	3	154.11 <sup>***</sup>	9.76 <sup>***</sup>	544.18 <sup>***</sup>	69.58 <sup>***</sup>	4.27 <sup>*</sup>	36.12 <sup>***</sup>	2.27 <sup>***</sup>	1.88 <sup>***</sup>
SCA	6	24.68 <sup>***</sup>	9.69 <sup>***</sup>	753.73 <sup>***</sup>	113.84 <sup>***</sup>	4.52 <sup>***</sup>	53.88 <sup>***</sup>	0.68 <sup>*</sup>	0.27 <sup>***</sup>
GCA/SCA	-	6.25	1.01	0.72	0.61	0.94	0.67	3.34	7.08
Error	18	4.29	2.96	134.07	23.14	4.25	12.90	0.07	0.25
C.V.	-	2.28	14.83	16.5	16.6		5.12	2.72	5.56

\*,\*\* Significantly different at 0.05 and 0.01 probability levels respectively.

### General combining ability effects ( $g_i$ )

Estimates of general combining ability effects ( $g_i$ ) and their standard errors for all traits are presented in Table 2. These estimates measure the differential ( $g_i$ ) contribution of the parents in relation to one another. None of the parents had consistently high  $g_i$  effects for all eight traits. Selection 07690 Nic had the largest  $g_i$  for plant height, number of spikes, biomass and grain yield. Parus had the highest  $g_i$  for protein content and the second largest  $g_i$  for biomass, number of spikes, and grain yield. Cak-Mak and Wd-Neb 021 had the largest positive  $g_i$  effects for kernel weight and harvest index, respectively. The mean values for parents and F1's crosses are presented in Table 3. The largest mean values for plant height and number of spikes were observed for selection 07690 Nic. Cak-Mak has the largest mean values for biomass, grain yield, number of kernels per spike, and kernel weight. High mean values for harvest index and protein content were noted in Parus.

The mean performance of parents (Table 3) and their  $g_i$  effects (Table 2) were inconsistent suggesting that the performance of the parents per se may not be reliable predictor of their value as parents for some traits. This is because additive genetic variance alone did not account for all genetic variability. Selection 07690 Nic had the highest mean values for plant height, and number of spikes, which were consistent with  $g_i$  effects, but inconsistent for biomass, and grain yield. Whereas Cak-Mak had the highest mean values for biomass, grain yield, kernel number and kernel weight, but had the highest  $g_i$  for only the latter two traits. The largest mean values for harvest index and protein content mean values were observed for Parus, however it only had the highest  $g_i$  for protein content. Wd-Neb 021 was not superior for any of the traits however, it did have the highest  $g_i$  for harvest index.



Table 2. Estimates for general combining ability ( $g_i$ ) effects for : plant height (HT), spike number (SP), biomass (BM), grain yield (GY), harvest index (HI), kernel number (KN), kernel weight (KW) and protein content (P) from a 4x4 diallel cross grown at East Farm in 1989-90.

Genotypes	HT (cm)	SP	BM (g)	GY (g)	HI (%)	KN	KW (g)	P (%)
Wd-Neb 021	-3.46**	-1.56*	-12.48	-4.40	1.02	1.32	-0.89**	-0.53**
Cak-Mak	-0.42	-0.42	-2.03	-0.97	-0.33	2.43	0.50**	-0.10
Parus	-3.42**	0.58	5.37	2.32	0.27	-0.57	0.09**	0.79**
07690 Nic	7.30**	1.40*	9.14	3.04	-0.95	-3.18	0.29**	-0.15**
S.E. ( $g_i$ )	0.87	0.60	27.37	4.72	0.66	2.63	0.01	0.05
S.E. ( $g_i - g_j$ )	1.16	0.81	36.49	6.30	0.87	3.51	0.02	0.07

\*, \*\*, significantly different from zero at 0.05 and 0.01 probability level respectively.

Table 3. Mean performance of F1 and parents for : plant height (HT), number of spike (SP), biomass (BM), grain yield (GY), harvest index (HI), kernel number (KN), kernel weight (KW) and protein content (P) evaluated at East Farm during the 1989-90 growing season.

Genotype	HT (cm)	SP	BM (g)	GY (g)	HI (%)	KN	KW (g)	P (%)
Wd-Neb 021	80.59	6.78	33.43	14.02	42.32	68.74	7.39	8.33
Cak-Mak	89.15	10.48	62.39	25.03	41.10	71.70	10.29	9.42
Parus	81.11	9.00	50.34	21.34	42.57	59.56	9.20	11.13
07690 Nic	98.44	11.33	59.89	23.81	39.88	56.37	9.42	8.66
Wd-Neb 021//Cak-Mak	88.44	9.85	59.40	25.21	42.74	72.56	9.83	7.92
Wd-Neb 021//Parus	83.26	12.26	67.90	31.57	47.01	77.22	9.36	8.97
Wd-Neb 021//07690 Nic	99.22	13.00	81.96	34.07	42.73	71.48	9.78	8.45
Cak-mak//Parus	84.96	12.59	82.57	33.53	40.87	76.48	10.64	9.01
Cak-Mak//07690 Nic	98.63	12.07	72.03	30.43	43.19	72.93	11.00	8.81
Parus//07690 Nic	101.89	18.63	132.04	51.29	39.61	74.59	11.20	9.69
LSD <sub>0.05</sub>	3.55	2.95	19.86	8.25	3.07	6.16	0.46	0.86

This lack of agreement between mean values observed in the parents and their corresponding  $g_i$  effects for the different traits could be due epistatic effects and/or preponderance of dominance effects (Singh et al. 1992). Moreover, none of the parental cultivars exhibited a significant  $g_i$  effects for biomass, grain yield, harvest index, and number of kernels per spike. Therefore, no definite inferences can be drawn as to the contribution of these parents for these traits. Nevertheless, Cak-Mak, Parus, and 07690 Nic exhibited a positive and highly significant  $g_i$  effects for kernel weight suggesting that the opportunity to improve this trait using these parents exists. Both 07690 Nic and Parus can be used to improve number of spikes per plant and protein content, respectively. The spring tall cultivar 07690 Nic was found to be the best combiner for increased plant height while the semi-dwarf selection Wd-Neb 021 and Parus were shown to be good combiners for short stature.

There were parents that produced progeny that performed better than expected based on mean parental performance as noted in the cross Parus//07690 Nic. This could be explained if the favorable genes are dispersed among the parents, thus the hybrid would possess a greater number of favorable genes for increasing most traits. The increased mean values for plant height, kernel weight, and protein content obtained in most crosses could be the result of additivity over loci and/or complementary interaction between loci (epistasis) (Sokol and Baker (1977).

#### Specific combining ability effects ( $s_{ij}$ )

Specific combining ability reflects the deviation of the performance of a cross from its expected mean value based on  $g_i$  effects and is considered a measure of non additive gene action. Estimates of  $s_{ij}$  for the six crosses are presented in Table 4. Most crosses except,

Cak-Mak//07690 Nic had positive  $s_{ij}$  effects for number of spikes, biomass and grain yield. High  $s_{ij}$  effects for plant height, number of spikes, biomass, grain yield, and kernel weight was noted in the cross Parus//07690 Nic. Significant  $s_{ij}$  effects for harvest index was noted in the crosses Wd-Neb 021//Parus and Cak-Mak//07690 Nic. Both were associated with intermediate  $s_{ij}$  effects for kernel number, kernel weight and biomass. A highly significant and positive  $s_{ij}$  for kernel weight was noted in all crosses suggesting that both additive and non-additive gene action are important in the inheritance of this trait. The largest  $s_{ij}$  for this trait were observed in crosses involving 07690 Nic. Negative and significant  $s_{ij}$  estimates were noted among winter x winter crosses for protein content indicating dominance toward the parent with lower protein content.

Lack of agreement between the mean values (Table 3) and non significant  $s_{ij}$  effects (Table 4) for protein content in winter x spring crosses suggested that the non-additive gene action is not important in predicting the performance of these crosses. A potential for a high frequency of transgressive segregates for protein content exists in these crosses due to complementary genes from spring and winter cultivars. High mean values and  $s_{ij}$  estimates for plant height were found in most crosses except Wd-Neb 021//Cak-Mak and Cak-Mak//07690 Nic. The cross Parus//07690 Nic had the greatest mean values and  $s_{ij}$  effects for number of spikes, biomass, and kernel weight. Agreement between mean value and  $s_{ij}$  effects for grain yield were also obtained in the cross Parus//07690 Nic and the cross Wd-Neb 021//07690 Nic. Agreement between mean values and  $s_{ij}$  were obtained for harvest index in most crosses except Wd-Neb//Cak-Mak and Wd-Neb 021// 07690 Nic. The highest mean value and  $s_{ij}$  estimate for harvest index were noted in the cross Wd-Neb 021// Parus, the lowest mean value and  $s_{ij}$  estimates were obtained in the cross Parus// 07690 Nic. Only estimates from the cross Cak-Mak//07690 Nic were in accord for number of kernels per spike.

Agreement between mean values and  $s_{ij}$  could indicate that deviations of crosses from the parental values might be important in predicting cross performance particularly, when  $s_{ij}$  estimates were significant. Since, the expression of number of spikes, biomass, grain yield, harvest index, and number of kernels per spike were predominately controlled by non-additive gene action, this could mislead the breeder when attempting to identify the best cross combination for these traits in early generation.

In self-pollinated crops heterozygosity is expected to decline rapidly in advanced generations, and in the absence of selection, the progeny mean is expected to approach the mid-parent value. Therefore, the specific combining ability ( $s_{ij}$ ) would not contribute in the improvement of self-pollinated crops like durum wheat except for the portion due to epistatic additive x additive (Bhullar et al. 1979). Quick (1978) reported that maximum yield in durum wheat may be obtainable only with a breeding system that could exploit both additive and non-additive effects. Such a breeding system may involve the production of hybrid wheat. However, (Bhullar et al. 1979) reported that in cases where crosses showing high  $s_{ij}$  effects are derived from parents with high  $g_i$  effects, direct exploitation of both additive and non additive gene effects is possible using conventional breeding methods. Complementary genes from two parents may be responsible for the observed non additive gene effect where a larger proportion seems to be due to additive x additive effects. In addition, to selecting parental lines on the basis of their  $g_i$  effects one should choose crosses with high  $s_{ij}$  effects.

The cross Parus//07690 Nic had the largest positive  $s_{ij}$  effects for most traits except harvest index. It had the highest mean values for plant height, biomass, number of spikes per plant, grain yield, kernel weight, and protein content. Agreement between the mean values,  $s_{ij}$  effects, and  $g_i$  effects of the parents for plant height, kernel weight, and protein content, indicated that both additive and non-additive gene action contributed to the variability of these

traits in this cross; however, gene action is most important besides the contribution of non-additive gene action for plant height, kernel weight, and protein content. This is because the parents with high  $g_i$  effects had also high mean values for these traits. Both parental cultivars involved in this cross had the highest  $g_i$  effects for number of spikes, biomass, grain yield. If a major portion of epistatic interactions involved in this cross are of additive x additive nature, it is expected that one should capitalize on a large percentage of the total genetic variability present. However a large  $s_{ij}$  for number of kernels per spike was noted in this cross although both parents had negative  $g_i$  effects for this trait. This indicated that improving number of kernels per spike would be limited.

Table 4. Estimates for specific combining ability effects ( $s_{ij}$ ) for : plant height (HT), spike number (SP), biomass (BM), grain yield (GY), harvest index (HI), kernel number (KN), 200 kernels weight (KW) and protein content (P) of the 4x4 diallel cross grown at East Farm in 1989-90.

Genotypes	HT (cm)	SP	BM (g)	GY (g)	HI (%)	KN	KW (g)	P (%)
Wd-Neb 021//Cak-Mak	1.75	0.23	3.72	1.55	-0.15	-1.35	0.41**	-0.48**
Wd-Neb 021//Parus	-0.44	1.63*	4.81	4.59	3.52**	6.31	0.35**	-0.32**
Wd-Neb 021//07690 Nic	4.81**	1.56	15.10	6.37	0.46	3.18	0.54**	0.10
Cak-Mak//Parus	-1.77	0.83	9.04	3.16	-1.27	4.46	0.24**	-0.72**
Cak-Mak//07690 Nic	1.18	-0.50	-5.27	-0.66	2.28*	3.52	0.40**	0.03
Parus//07690 Nic	7.44**	5.05**	47.34	16.90*	-1.91*	8.18*	1.01**	0.01
S.E. ( $S_{ij}$ )	5.73	3.96	179.50	30.96	4.30	17.27	0.10	0.34
S.E. ( $S_{ij}$ )	3.12	2.16	97.91	16.90	2.35	9.42	0.05	0.18
S.E. ( $s_{ij}-s_{ik}$ )	5.82	4.03	182.44	31.48	4.37	17.55	0.10	0.34
S.E. ( $s_{ij}-s_{kl}$ )	4.66	3.22	145.95	25.19	3.50	14.04	0.08	0.28

\*, \*\*, significantly different from zero at 5% and 1% probability level respectively.

### Mean Generations Analysis

To further evaluate the nature of gene action involved in the inheritance of the different traits, mean generations analysis was carried out based on five populations (two parents, F1, F2, and F3 generations) within each of the six crosses.

Analyses of variance for the five generations in each cross evaluated at Ruggs and at East Farm experimental sites are presented in Appendix, Tables 6 and 7 respectively. Results from the analysis of variance indicated a lack of consistent differences in the five generations (two parents, F1, F2, and F3) for all traits within each of the six crosses when both sites are compared. This lack of consistency might be attributed to the effect of the genotype x environment interactions and to sampling errors.

At Ruggs, significant differences for plant height were observed in all crosses except Wd-Neb 021//Cak-Mak. This can be attributed to a similarity in genetic factors for plant height by the two parents and their progenies F1, F2 and F3. The five generations differed significantly for number of spikes in Wd-Neb 021//Cak-Mak, Wd-Neb 021//Parus, Cak-Mak//07690 Nic and Parus//07690 Nic crosses. Biomass was significant in crosses involving the parent Wd-Neb 021. This parent seemed to contribute to the variability of grain yield in most crosses with the exception of the cross Wd-Neb 021//Cak-Mak where the five generations did not differ significantly. Harvest index was significant in only two crosses, Wd-Neb 021//Cak-Mak and Parus//07690 Nic. The five generations differed significantly for kernel weight and protein content in all crosses with the exception of cross Wd-Neb 021//Parus for kernel weight and the cross Cak-Mak//07690 Nic for protein content.

At East Farm, significant differences were noted in the six crosses for plant height; however, no consistent differences were detected in the six crosses for the other traits.



Differences were observed for number of spikes in Wd-Neb 021//Cak-Mak, Cak-Mak//Parus, Cak-Mak//07690 Nic, and Parus//07690 Nic. Biomass differences were found among all generations in crosses, Wd-Neb 021//Cak-Mak, Wd-Neb 021//Parus, Cak-Mak//Parus, and Parus//07690 Nic. The five generations differed significantly for grain yield in most crosses, except Cak-Mak//07690 Nic. Only generations from the cross Cak-Mak//07690 Nic differed significantly for harvest index. Differences in kernel weight were found in generations in crosses Wd-Neb 021//Parus, Wd-Neb 021//Parus, and Parus//07690 Nic. Protein content differences were significant in most crosses except Wd-Neb 021//Cak-Mak.

#### Detection of non allelic interaction

The validity of the different genetic components depends upon the presence of epistatic effects. Ketata (1976) reported that estimates of epistatic effects (when detected) in the inheritance of a trait are unique. Hayman (1958) proposed that an approximation of epistasis free estimates of the mean (m), additive (a), and dominance (d) would be those estimates obtained from the three parameter model. The adequacy of the three parameter model (mean, additive, dominance) or five parameter model (which include mean, additive, dominance, additive x additive, and dominance x dominance) are based on tests that allow detection of the presence or absence of epistasis.

The separate C, D, and joint (J) scaling tests are summarized in Appendix, Tables 8 and 9 for the six crosses evaluated at Ruggs and at East Farm, respectively. For a particular trait in the cross, a significant C test would indicate additive x additive epistatic effects, whereas a significant D test implies dominance x dominance effect. However, the joint scaling test (J) would detect either type of epistasis effects involved in the inheritance of a

particular trait. The joint scaling test is considered more precise in detecting epistatic effects than either C or D since it is based on information from all generations (Ketata et al. 1976). Consequently the three or five parameter models are fitted on the basis of the joint scaling test. It is noteworthy, however, that lack of significance detected by the tests does not necessarily imply the absence of non allelic interactions; rather, it suggests that these effects are too small to be detected by any of these tests (Mather and Jinks, 1982).

In the present investigation, there was an agreement between the joint scaling test and C or D tests for all traits studied. However, epistatic effects for protein effect in cross Parus// 07690 Nic evaluated at the Ruggs site were detected by C and D tests only. The C test was significant in the cross Wd-Neb 021//Cak-Mak for plant height evaluated at East Farm while D and J were not.

Estimates of genetic effects.

### Plant height

The joint scaling test indicated that epistasis was involved in the inheritance of plant height in crosses between semi-dwarf and tall cultivars such as Cak-Mak//Parus grown at Ruggs site, and Wd-Neb 021//07690 Nic, and Cak-Mak//07690 Nic grown at East Farm (Table 5). Therefore a five parameter model was needed to explain the genetic variability in these crosses. These results were in agreement with those reported by Amaya et al.(1972) who found that epistatic effects explained most of the variability in crosses involving semi-dwarf and tall parents in durum wheat. The three parameter model proved to be satisfactory for the rest of the crosses Wd-Neb 021//Cak-Mak, Wd-Neb 021//Parus, and Parus//07690 Nic

at both locations, and in crosses Wd-Neb 021//07690 Nic at the Ruggs site, and Cak-Mak//Parus evaluated East Farm.

The disparities observed between the two experiments might be attributed to differential responses of plant height to the environment. Estimates from the three parameter model at the Ruggs site indicated that dominance favoring taller plants contributed significantly to the inheritance of plant height in crosses Wd-Neb 021//07690 Nic, Cak-Mak//06790 Nic, and Parus//07690 Nic. These results suggest that selection 07690 Nic contributed to the variability for plant height in these populations. Greater additive effects were observed in the cross Wd-Neb 021//Parus. Lack of significance of genetic components was noted in the cross Wd-Neb 021//Cak-Mak. Estimates from the five parameter model showed that the additive and additive x additive effects made the largest contribution in the expression of plant height in the cross Cak-Mak//Parus.

At East Farm, the three parameter model indicated that dominance effects explained most of the variability for plant height in the cross Parus//07690 Nic. However, no significant effects were detected in crosses Wd-Neb 021//Cak-Mak, Wd-Neb 021//Parus, and Cak-Mak//Parus. Positive additive x additive and negative dominance x dominance from the five parameter model were larger than their respective standard errors and explained most of the genetic variability in cross Wd-Neb 021//07690 Nic. Negative dominance x dominance and additive effects described the variability of plant height in the cross Cak-Mak//07690 Nic. Dominance towards shorter plants and significant negative dominance x dominance suggested a preponderance of duplicate epistasis involved in the inheritance of plant height in crosses Cak-Mak//Parus and Cak-Mak//07690 Nic evaluated at Ruggs and at East Farm, respectively.

### Number of spikes, biomass, and grain yield

None of the three scaling tests provided evidence of epistatic effects for spike number, biomass, and grain yield evaluated at either Ruggs or East Farm. The three parameter model was satisfactory in explaining the genetic variability in all crosses evaluated at both locations for these traits (Tables 6, 7 and 8); however, neither additive nor dominance effects were significantly different from zero. This lack of significance might be attributed to either large sampling errors, association between the means and their respective variances, and/or genotype x environment interaction that inflated the different estimates.

Ketata et al. (1976) was not able to detect significant genetic variability in a study of one cross involving two winter wheat cultivars for number of spikes. Using mean generation analysis carried out on seven generations (two parents, F1, F2, F3 lines and two backcrosses), Amaya et al. (1972) found that dominance effects were predominant in controlling grain yield in four crosses of durum. However, they pointed out that these estimates were biased upward due to the genotype x environment interaction. Therefore, the preponderance of specific combining ability variances (SCA) from diallel analysis could be attributed to dominance effects and genotype by environment interaction as revealed by mean generation analysis. In addition, the lack of significance of genetic estimates for biomass could be attributed to compensatory effects operating on plant height, number of spikes, and other components of grain yield. Based on information gained from the generation mean analysis it is suggested that early generations selection for these traits would be ineffective due to the masking effects of dominance and genotype x environment interactions.

Table 5. Estimates of genetic effects for plant height in six crosses of durum wheat evaluated at Ruggs and East Farm during the growing seasons of 1991 and 1992, respectively.

Ruggs 1991						
Model	Wd-Neb 021//Cak-Mak	Wd-Neb 021 //Parus	Wd-Neb 021//07690 Nic	Cak-Mak//Parus	Cak-Mak//07690 Nic	Parus//07690 Nic
m	93.3 <sup>***</sup>	87.40 <sup>***</sup>	101.50 <sup>***</sup>	89.70 <sup>***</sup>	103.02 <sup>***</sup>	98.30 <sup>***</sup>
a	1.29	4.10 <sup>*</sup>	10.62 <sup>***</sup>	6.34 <sup>***</sup>	9.10 <sup>***</sup>	14.10 <sup>***</sup>
d	1.87	0.16	16.09 <sup>***</sup>	10.60 <sup>***</sup>	12.80 <sup>***</sup>	18.90 <sup>***</sup>
$\chi^2$	0.54	2.42	0.30	8.51	0.04	1.90
p	0.75-0.90	0.25-0.50	0.75-0.90	< 0.025	> 0.99	0.25-0.50
m				96.42 <sup>***</sup>		
a				15.28 <sup>*</sup>		
d				-28.57		
aa				70.03 <sup>*</sup>		
dd				-22.54		
East Farm 1992						
m	90.20 <sup>***</sup>	89.80 <sup>***</sup>	97.80 <sup>***</sup>	88.70 <sup>***</sup>	112.65 <sup>***</sup>	103.02 <sup>***</sup>
a	0.77	2.69	7.83 <sup>***</sup>	1.45	19.43 <sup>***</sup>	15.10 <sup>***</sup>
d	2.06	-5.1	12.5 <sup>***</sup>	3.18	0.20	11.03 <sup>***</sup>
$\chi^2$	5.14	3.69	23.24	0.66	6.54	3.07
p	0.05-0.10	0.10-0.25	< 0.005	0.75-0.90	0.025-0.05	0.10-0.25
m			98.14 <sup>***</sup>		111.95 <sup>***</sup>	
a			9.59 <sup>*</sup>		12.19 <sup>*</sup>	
d			10.24		-4.75	
aa			-54.72 <sup>*</sup>		11.71	
dd			30.57 <sup>*</sup>		-22.86 <sup>*</sup>	

\*,\*\* significantly different from zero at 5% and 1% level of probability respectively.

m= mean of the generations, a= estimate of additive effects, d= dominance effects aa= additive x additive effects, dd=dominance x dominance effects, p=probability levels,  $\chi^2$  = Chisquare.

Table 6. Estimates of genetic effects for spike number in six crosses of durum wheat evaluated at Ruggs and East Farm during the growing seasons of 1991 and 1992, respectively.

Ruggs 1991						
Model	Wd-Neb 021//Cak-Mak	Wd-Neb 021//Parus	Wd-Neb 021//07690 Nic	Cak-Mak//Parus	Cak-Mak//07690 Nic	Parus//07690 Nic
m	25.30**	24.30**	24.30**	27.10**	26.90**	25.50**
a	3.01	1.6	1.34	1.34	1.81	0.42
d	5.4	-0.06	0.25	1.29	0.36	-3.2
$\chi^2$	0.21	0.30	0.09	0.09	0.36	0.23
p	0.90-0.90	0.75-0.90	0.975-0.99	0.975-0.99	0.75-0.90	0.90-0.95
East Farm 1992						
m	12.30**	10.60**	11.70**	11.60**	12.70**	10.40**
a	1.18	0.56	0.63	1.62	0.53	0.69
d	-0.20	1.1	-0.6	2.28	-1.9	-0.90
$\chi^2$	0.03	0.13	0.16	0.44	0.02	1.15
p	>0.99	0.9-0.95	0.90-0.95	0.75-0.90	>0.99	0.75-0.90

\*\* significantly different from zero at 1% level of probability

m= mean of the generations, a= estimate of additive effects, d= dominance effects aa= additive x additive effects, dd=dominance x dominance effects, p=probability levels,  $\chi^2$  = Chisquare

Table 7. Estimates of genetic effects for biomass in six crosses of durum wheat evaluated at Ruggs and East Farm during the growing seasons of 1991 and 1992, respectively.

Ruggs 1991						
Model	Wd-Neb 021//Cak-Mak	Wd-Neb 021//Parus	Wd-Neb 021//07690 Nic	Cak-Mak//Parus	Cak-Mak//07690 Nic	Parus//07690 Nic
m	124.06**	121.03**	133.4**	133.01**	136.02**	131.04**
a	8.23	6.73	12.41	0.82	2.48	1.52
d	32.6	7.32	-3.23	5.92	3.36	-0.9
$\chi^2$	0.43	0.41	0.23	0.38	0.22	0.13
p	0.75-0.90	0.75-0.90	0.75-0.90	0.75-0.90	0.75-0.90	0.90-95
East Farm 1992						
m	85.90**	82.90**	90.10**	83.60**	97.70**	82.9**
a	3.66	1.25	5.67	3.9	2.16	4.78
d	6.04	6.75	0.47	10.4	-5.6	-0.30
$\chi^2$	0.4	0.15	0.23	0.87	0.12	1.23
p	0.75-0.90	0.90-0.95	0.75-0.90	0.50-0.75	0.90-0.95	0.50-0.75

\*\* significantly different from zero at 1% level of probability.

m= mean of the generations, a= estimate of additive effects, d= dominance effects aa= additive x additive effects, dd=dominance x dominance effects, p=probability levels,  $\chi^2$  = Chisquare

Table 8. Estimates of genetic effects for grain yield in six crosses of durum wheat evaluated at Ruggs and East Farm during the growing seasons of 1991 and 1992, respectively.

Ruggs 1991						
Model	Wd-Neb 021//Cak-Mak	Wd-Neb 021//Parus	Wd-Neb 021//07690 Nic	Cak-Mak//Parus	Cak-Mak//07690 Nic	Parus//07690 Nic
m	40.01**	42.03**	43.68**	46.90**	46.50**	43.60**
a	4.44	3.92	2.45	1.50	3.40	1.50
d	5.66	-0.30	-4.29	8.17	-8.60	0.76
$\chi^2$	0.18	0.24	0.35	0.07	0.09	0.02
p	0.90-0.95	0.75-0.90	0.75-0.90	0.95-0.975	0.95-0.975	< 0.99
East Farm 1992						
m	29.50**	27.4**	30.60**	28.01**	33.30**	28.40**
a	0.58	1.54	2.24	2.13	1.80	3.38
d	1.77	2.1	-0.7	5.55	-2.5	1.97
$\chi^2$	0.15	0.17	0.68	0.13	0.02	0.63
p	0.90-0.95	0.90-0.95	0.75-0.90	0.90-0.95	> 0.99	0.75-0.90

\*\* significantly different from zero at 1% level of probability.

m= mean of the generations, a= estimate of additive effects, d= dominance effects aa= additive x additive effects, dd=dominance x dominance effects, p=probability levels,  $\chi^2$  = Chisquare



## Harvest index

The joint scaling test indicated that epistasis was involved in the inheritance of harvest index in crosses Wd-Neb 021//Cak-Mak and Cak-Mak//Parus at Ruggs site and only in cross Wd-Neb 021//07690 Nic evaluated at East Farm. Based on the three parameter model, dominance and additive effects were equally important in the expression of harvest index in the cross Parus//07690 Nic at Ruggs. Additive gene action was more important than dominance estimates in the cross Wd-Neb 021//Parus, whereas, pronounced dominance effects were observed in crosses and Cak-Mak//Parus (Table 9). None of the genetic estimates differed significantly from their respective standard errors in crosses Wd-Neb 021//07690 Nic, Cak-Mak//07690 Nic at the Ruggs site. These crosses involved selection 07690 Nic, the tallest parent, and the two shortest parents, Wd-Neb 021 and Parus. Increased plant height might have contributed to the reduced harvest index in these crosses. At East Farm, estimates from the three parameter model were not significant in crosses Wd-Neb 021//Cak-Mak, Wd-Neb 021//Parus, Cak-Mak//Parus, Cak-Mak//07690 Nic, and Parus//07690 Nic. These results suggest that the influence of environment and compensatory effects may have contributed to the lack of significance of the different genetic components.

Due to epistasis, the five parameter model was invoked to explain the genetic variation in crosses Wd-Neb 021//Cak-Mak and Cak-Mak//Parus evaluated at Ruggs site and in cross Wd-Neb 021//07690 Nic at East Farm. Dominance effects exerted a greater role in the inheritance of harvest index in crosses Wd-Neb 021//Cak-Mak and Cak-Mak//Parus at Ruggs. Positive dominance and negative dominance x dominance effects explained most of the variability in the cross Wd-Neb 021//07690 Nic at East Farm suggesting duplicate epistatic effects for this trait.

Table 9. Estimates of genetic effects for harvest index in six crosses of durum wheat evaluated at Ruggs and East Farm during the growing seasons of 1991 and 1992, respectively.

Ruggs 1991						
Model	Wd-Neb 021//Cak-Mak	Wd-Neb 021 // Parus	Wd-Neb 021//07690 Nic	Cak-Mak//Parus	Cak-Mak // 07690 Nic	Parus// 07690 Nic
m	25.01 <sup>***</sup>	32.3 <sup>***</sup>	31.8 <sup>***</sup>	31.5 <sup>***</sup>	32.4 <sup>***</sup>	33.00 <sup>***</sup>
a	0.70	2.47 <sup>*</sup>	-0.17	-2.70 <sup>*</sup>	1.11	1.76 <sup>*</sup>
d	4.60 <sup>***</sup>	-0.50	-1.56	7.72 <sup>***</sup>	-3.30	1.75 <sup>*</sup>
$\chi^2$	19.22	0.29	3.26	7.94	1.03	3.08
p	<0.01	0.75-0.90	0.10-0.25	<0.025	0.5-0.75	0.10-0.25
m	29.31 <sup>***</sup>			36.78 <sup>***</sup>		
a	-2.11			0.17		
d	9.83 <sup>***</sup>			12.79 <sup>***</sup>		
aa	-15.57			-14.91		
dd	13.06			5.14		
East Farm 1992						
m	34.1 <sup>**</sup>	32.60 <sup>***</sup>	32.60 <sup>***</sup>	33.90 <sup>***</sup>	33.60 <sup>***</sup>	33.70 <sup>***</sup>
a	0.68	1.49	0.17	0.03	1.33	1.64
d	-1.3	0.17	6.73 <sup>***</sup>	0.36	-2.8	2.25
$\chi^2$	0.9	0.39	13.28	3.02	0.27	0.27
p	>0.95	0.90-0.95	<0.005	0.5-0.75	0.75-0.90	0.75-0.90
m			31.02 <sup>***</sup>			
a			0.92			
d			0.35			
aa			18.21			
dd			-21.67 <sup>***</sup>			

\*,\*\* significantly different from zero at 5% and 1% level of probability respectively.

m= mean of the generations, a= estimate of additive effects, d= dominance effects aa= additive x additive effects, dd=dominance x dominance effects, p=probability levels,  $\chi^2$  = Chisquare

## Kernel weight

Based on the joint scaling test, a five parameter model was required to determine the nature of gene action controlling kernel weight in crosses Wd-Neb 021//Cak-Mak, Wd-Neb 021//Parus, Cak-Mak//07690 Nic, and Parus//07690 Nic at the Ruggs site and the cross Wd-Neb 021//Parus at East Farm (Table 10). Lack of significance of genetic estimates based on the three parameter model was noted in cross Wd-Neb 021//07690 Nic at Ruggs and crosses Cak-Mak//Parus, Cak-Mak//07690 Nic, and Parus//07690 Nic at East Farm. However, dominance effects explained most of the variability for kernel weight in crosses Cak-Mak//Parus and Wd-Neb 021//Cak-Mak evaluated at Ruggs and East Farm, respectively.

Estimates of genetic components from the five parameter model for the experimental material at the Ruggs site showed that additive gene action had the most pronounced effect on kernel weight in cross Wd-Neb 021//Cak-Mak suggesting that gain from selection in early generation for kernel weight is possible in this material. Most of the genetic estimates were significant in cross Wd-Neb 021//Parus where negative additive x additive and the positive dominance effects made the largest contribution in the inheritance of kernel weight. At Ruggs, significant and positive additive x additive effects were observed in crosses Cak-Mak//07690 Nic. However negative additive x additive estimates was noted in the cross Parus//07690 Nic, at the same site. A preponderance of additive x additive components coupled with dominance toward lighter kernel weight were observed in the cross Wd-Neb 021//Parus at East Farm. Sun et al. (1972) reported nonallelic interactions involved in the inheritance of kernel weight in a study of six crosses of bread wheat.

Table 10. Estimates of genetic effects for kernel weight in six crosses of durum wheat evaluated at Ruggs and East Farm during the growing seasons of 1991 and 1992, respectively.

Ruggs 1991						
Model	Wd- Neb 021//Cak-Mak	Wd-Neb 021//Parus	Wd-Neb 021//07690 Nic	Cak-Mak//Parus	Cak-Mak//07690 Nic	Parus//07690 Nic
m	8.60 <sup>***</sup>	7.72 <sup>**</sup>	7.70 <sup>***</sup>	9.03 <sup>***</sup>	8.97 <sup>**</sup>	8.91 <sup>**</sup>
a	0.96 <sup>***</sup>	0.35 <sup>***</sup>	0.25	0.24	0.31 <sup>*</sup>	0.18
d	0.74 <sup>*</sup>	0.48 <sup>*</sup>	0.28	0.56 <sup>***</sup>	0.33	1.84 <sup>***</sup>
$\chi^2$	7.03	30.76	3.15	2.45	5.67	30.12
p	0.25-0.50	<0.01	0.10-0.25	0.25-0.50	0.05-0.10	<0.01
m	8.98 <sup>***</sup>	8.12 <sup>***</sup>			9.23 <sup>***</sup>	9.48 <sup>***</sup>
a	0.84 <sup>***</sup>	0.60 <sup>***</sup>			0.29	0.06
d	-0.87	1.68 <sup>***</sup>			1.01	-0.24
aa	0.51	-2.88 <sup>***</sup>			-3.31 <sup>*</sup>	6.08 <sup>***</sup>
dd	-0.67	0.32 <sup>***</sup>			0.82	-0.76

  

East Farm 1992						
m	8.45 <sup>**</sup>	9.46 <sup>***</sup>	9.4 <sup>***</sup>	9.71 <sup>***</sup>	9.93 <sup>***</sup>	9.84 <sup>***</sup>
a	0.21	1.20 <sup>***</sup>	1.16 <sup>***</sup>	0.02	0.64	0.70
d	0.72 <sup>***</sup>	0.004	0.20	0.42	0.69	1.50
$\chi^2$	2.82	9.71	1.63	0.10	2.05	4.81
p	0.25-0.50	0.01-0.025	0.25-0.50	>0.95	0.25-0.50	0.10-0.25
m		9.34 <sup>***</sup>				
a		0.68				
d		-2.31 <sup>***</sup>				
aa		5.17 <sup>***</sup>				
dd		-0.20				

\*,\*\* significantly different from zero at 5% and 1% level of probability respectively.

m= mean of the generations, a= estimate of additive effects, d= dominance effects aa= additive x additive effects, dd=dominance x dominance effects, p=probability levels,  $\chi^2$ = Chisquare

## Protein content

Epistatic effects for protein content were detected in crosses Wd-Neb 021//Cak-Mak, Wd-Neb 021//Parus, and Cak-Mak//07690 Nic at both Ruggs and East Farm and in cross Cak-Mak//Parus only at East Farm. The five parameter model was needed to explain the genetic variability in these crosses. The simple additive-dominance model was adequate to describe the variation in Wd-Neb 021//07690 Nic and Parus//07690 Nic crosses at both locations and in cross Cak-Mak//Parus at the Ruggs site (Table 11).

Based on the three parameter model, dominance effects favored lower protein content in crosses Wd-Neb 021//07690 Nic and Cak-Mak//Parus. These results were in agreement with those reported by Bhullar et al. (1978). Greater additive effects were observed in the cross Parus//07690 Nic at the Ruggs site. Estimates in crosses Wd-Neb 021//07690 Nic and Parus//07690 Nic showed that both additive and dominance effects were involved in the inheritance of protein percentage with dominance effects being more predominant at East Farm. Inconsistencies in estimates of the genetic components indicated that these estimates were influenced by genotype x environment interaction as shown for cross Parus//07690 Nic. Mostly dominance, additive x additive, and dominance x dominance effects contributed to the variation of protein content in Wd-Neb 021//Cak-Mak, Wd-Neb 021//Parus, Cak-Mak//07690 Nic crosses at both locations, and in the cross Cak-Mak//Parus at East Farm. However, their sign and magnitude were not consistent. The negative dominance and positive dominance x dominance components observed in the cross Wd-Neb 021//Parus at both locations suggest evidence of duplicate epistasis for this trait (Bhullar et al. 1978). Therefore early generation selection for protein content in this material could be ineffective.

Table 11. Estimates of genetic effects for protein content in six crosses of durum wheat evaluated at Ruggs and East Farm during the growing seasons of 1991 and 1992, respectively.

Ruggs 1991						
Model	Wd-Neb 021//Cak-Mak	Wd-Neb 021//Parus	Wd-Neb 021//07690 Nic	Cak-Mak//Parus	Cak-Mak//07690 Nic	Parus//07690 Nic
m	15.10 <sup>***</sup>	13.50 <sup>***</sup>	14.06 <sup>***</sup>	14.4 <sup>***</sup>	14.2 <sup>***</sup>	14.8 <sup>***</sup>
a	-1.10 <sup>***</sup>	1.14 <sup>***</sup>	-0.01	0.56 <sup>***</sup>	0.02	0.68 <sup>***</sup>
d	-3.01 <sup>***</sup>	-1.01 <sup>***</sup>	-0.46	-1.10 <sup>***</sup>	0.55 <sup>***</sup>	-0.23 <sup>***</sup>
$\chi^2$	63.91	7.13	1.70	3.9	31.68	4.64
p	<0.01	<0.05	0.25-0.50	0.10-0.25	<0.01	0.05-0.10
m	12.85 <sup>***</sup>	12.73 <sup>***</sup>			14.59 <sup>***</sup>	
a	-0.38	0.89			0.15	
d	-5.13 <sup>***</sup>	-1.41 <sup>***</sup>			-0.65	
aa	7.65 <sup>***</sup>	2.19 <sup>*</sup>			-1.50	
dd	-1.33	2.18 <sup>***</sup>			-0.77 <sup>*</sup>	
East Farm 1992						
m	10.4 <sup>***</sup>	10.03 <sup>***</sup>	11.3 <sup>***</sup>	11.60 <sup>***</sup>	11.70 <sup>***</sup>	12.60 <sup>***</sup>
a	0.44	1.25 <sup>***</sup>	2.46 <sup>***</sup>	0.80 <sup>***</sup>	1.93 <sup>***</sup>	1.10 <sup>***</sup>
d	-0.3	-0.65 <sup>*</sup>	-2.50 <sup>***</sup>	1.50 <sup>***</sup>	-2.70 <sup>***</sup>	-3.40 <sup>***</sup>
$\chi^2$	9.71	9.05	4.16	20.64	39.68	1.48
p	0.01-0.025	0.01-0.025	0.10-0.25	<0.005	0.25-0.50	0.25-0.50
m	10.1 <sup>***</sup>	9.35 <sup>***</sup>		11.29 <sup>***</sup>	10.42 <sup>***</sup>	
a	-0.77 <sup>***</sup>	1.41 <sup>*</sup>		0.64 <sup>*</sup>	1.52 <sup>***</sup>	
d	-2.3 <sup>*</sup>	-1.41 <sup>***</sup>		0.75	-1.87 <sup>***</sup>	
aa	2.32	3.79 <sup>*</sup>		-6.75 <sup>***</sup>	-1.57	
dd	-2.84 <sup>*</sup>	3.35 <sup>*</sup>		0.73	3.91 <sup>***</sup>	

\*,\*\* significantly different from zero at 5% and 1% level of probability respectively.

m= mean of the generations, a= estimate of additive effects, d= dominance effects aa= additive x additive effects, dd=dominance x dominance effects, p=probability levels,  $\chi^2$ = Chisquare

Results from this study suggested that genotype x environment interactions appeared to influence the expression of most of the traits. These interactions were found to be extreme so that genetic estimates from a mean generation analysis were unique at each site and within each cross. The degree and direction of genetic estimates for most traits were genotype (depending on the genetic background of a cross) and environment specific. Although, additive effects from mean generation analysis should be free from linkage bias, these estimates depended on the sample size, the magnitude of sampling errors, and the genotype x environment interactions. The lack of significance of additive effects implied that genes of like effect were dispersed between the parental cultivars for most traits. However, all models that fit the means of the five generations gave an indication that selections Cak-Mak, Parus, and 07690 Nic had contributed to the variability observed for plant height, harvest index, kernel weight and protein content. Further evaluations using additional segregating populations including backcrosses are needed to provide more accurate estimates of genetic estimates and possible predictions of transgressive segregates. Nevertheless, mean generation analysis revealed that dominance and epistasis were involved in the inheritance of plant height, kernel weight, harvest index, and protein content in some crosses. This substantiated the lack of agreement between mean performance of the parents and their  $g_i$  effects for these traits.

Because of the inconsistencies of genetic estimates from mean generation analysis, combining ability analysis appeared to provide more adequate estimates of gene action for most traits. The genetic divergence between spring and winter type durum wheats reflected in their contrasting morphology could explained their genetic complementarity resulting in high  $g_i$  effects for plant height, grain yield, kernel weight and protein content. Finally, GCA/SCA ratio suggested that direct selection for plant height, kernel weight, and protein content in early generations is possible in this material.

## **Study 2. Possible Associations Between Grain yield and Protein Content and Efficiency of Early Generations Selection**

The major objectives in durum wheat breeding programs include the improvement of grain yield and protein content. To achieve these goals, the breeder has the option of selecting superior genotypes in early segregating populations or delaying intense selection until advanced generations when progenies are nearly homozygous. The most critical factors affecting the efficiency of selection in segregating populations for grain yield and protein content include the genetic diversity between the parental cultivars and the nature of inheritance of these traits. By knowing the magnitude and nature of the prevalent genetic variation controlling the expression of these traits, the breeder can efficiently allocate resources and efforts in selecting only in the most promising crosses. A superior cross must have a large genetic variance with an acceptable mean value. It was the objectives of this study to identify potential crosses on the basis of their performances, evaluate the reliability of individual plant selection from segregating populations, and identify possible associations between selection criteria for grain yield and protein content in F3 and F4 lines.

### **Means and Variances within F3 and F4 Lines**

Observed mean squares of the combined analysis of variance for each of the F3 and F4 lines are provided in Appendix, Tables 10 and 11. Significant genetic variation was found in both F3 and F4 lines as well as for the lines x location interactions for all traits except harvest index. The analysis of variance within location indicated that differences among lines existed for all traits except harvest index in both F3 and F4 lines (Appendix, Tables 12 and



13). Varying productivity within F3 and F4 segregating populations resulting from inter-genotypic competition could be the cause of the failure to detect significant differences for harvest index (Donald and Hamblin, 1976; McVetty and Evans, 1980). For example, increased plant height in F3 lines from crosses involving selection 07690 Nic was associated with lower biomass and grain yield at Ruggs (Table 12). Lower grain yield could be attributed to the limited number of spikes per plant and number of kernels per spike. In contrast, semi-dwarf lines were associated with higher biomass and grain yield particularly in F3 lines from Wd-Neb 012//Parus and Cak-Mak//Parus evaluated at the Ruggs experimental site. Whether differential competition effects or compensation among plant height and components of yield do occur, the lack of genetic variability of harvest index noted in both generations suggested that this trait is of a little value when assessed in solid stand conditions.

The mean values within location for each of the F3 and F4 lines within crosses are presented in Tables 12 and 13, respectively. The highest means for plant height were observed in crosses involving selection 07690 Nic (spring type) at both locations. In addition, lines from these crosses were also associated with higher kernel weight, and protein content in F3 and F4 lines at both locations. Greater mean values for biomass and grain yield in F3 lines were noted in the cross Wd-Neb 021//Parus at Ruggs. A higher mean value for grain yield was observed in lines from the cross Cak-Mak//07690 Nic at East Farm. In the F4 lines, the largest and most consistent mean values for biomass and grain yield were observed in the progenies from the cross Wd-Neb 021//Parus at both locations. It is noted that the higher mean values for most of the traits within each cross are in agreement with combining ability estimates. It appears that Cak-Mak, Parus, and 07690 Nic have contributed in additive fashion to the expression of most traits. Nevertheless, discrepancies were noted at both locations. The F3 lines from winter x spring crosses were associated with lower mean values

for biomass and grain yield than those from winter x winter crosses at Ruggs but not at East Farm (Table 12).

Higher mean values were found at East Farm than at the Ruggs site for all traits except protein content. At the Ruggs site, protein content mean values exceeded those observed at East Farm by 3% and 2.7% in F3 and F4 lines, respectively. Leaf diseases (rusts) and dry conditions during the grain filling may have resulted in lighter more shrivelled kernels in some genotypes (Tables 12 and 13). Since poorly filled kernels have been reported to be associated with higher protein content than plump kernels in bread wheat (Croy et al. 1978), it is expected that genetic differences in protein content were probably confounded by inadequate kernel development at the Ruggs site. The increased grain yield at East Farm may have caused a dilution of a limited amount of protein content deposited in a larger number of kernels per spike. Since protein content is a concentration trait, it is possible that an increase in grain yield without a proportional increase of protein translocated to the developing grain resulted in a lower protein content at East Farm.

The coefficients of variation (CV) associated with biomass, grain yield, harvest index, and kernel weight were larger at the Ruggs site than those observed at East Farm in both the F3 and F4 lines. These results may have been due to lodging of several row plots of crosses involving the tall parent 07690 Nic at Ruggs. Also, drought stress occurring during the grain filling stage at the Ruggs site may have accounted for the large error variance. Ceccarelli et al. (1991) reported that such stresses are usually associated with large environmental errors increasing the difficulty in relating phenotype with genotype. Plant height and protein content were found to be associated with higher CV at East Farm than at Ruggs in both F3 and F4 lines. The high heterogeneity and higher frequency of transgressive segregates could explain the greater CV in the F3 than in F4 lines noted for most traits at both locations.

Growing conditions at Ruggs promoted the expression of biomass and grain yield in F3 lines from winter x winter crosses but had an adverse effect on the performance of winter x spring crosses. Differential winter hardiness in the material may be responsible for these differences. Mild winter conditions at East Farm may have contributed to the higher mean values of most traits in spring x winter lines. Similar results were reported by Randhawa and Gill (1980). These authors found that crosses from early generations involving winter x spring crosses of bread wheat did not outyield spring x spring crosses in spring growing conditions.

Table 12. Mean values for plant height (HT), biomass (BM), grain yield (GY), harvest index (HI), kernel weight (KW), and protein content (P) in F3 lines within crosses evaluated at Ruggs and East Farm during the growing season 1992.

Genotype	Ruggs						East Farm					
	HT (cm)	BM (g)	GY (g)	HI (%)	KW (g)	P (%)	HT (cm)	BM (g)	GY (g)	HI (%)	KW (g)	P (%)
Wd-Neb 021//Cak-Mak	87.1	515.8	166.5	32.5	8.1	12.0	100.4	598.8	201.9	33.9	8.8	9.1
Wd-Neb 021//Parus	92.3	562.5	183.7	33.6	8.2	11.7	105.5	645.3	221.9	34.6	8.9	8.9
Wd-Neb 021//07690 Nic	107.7	508.2	138.8	28.0	7.3	13.5	126.6	635.7	213.4	33.7	8.8	9.5
Cak-Mak//Parus	92.1	545.3	179.6	33.5	9.5	11.8	96.4	536.9	175.7	32.7	9.4	10.0
Cak-Mak//07690 Nic	107.9	466.0	146.2	31.3	8.9	13.7	129.7	593.8	223.4	37.9	10.0	10.1
Parus//07690 Nic	113.7	478.9	174.1	36.8	9.3	12.9	130.6	611.7	214.1	35.5	10.3	10.3
LSD0.05	3.4	40.1	12.8	2.2	0.3	0.3	4.7	33.9	14.1	1.7	0.2	0.3
C.V	9.3	21.7	21.6	19.1	9.5	5.9	11.4	15.6	18.8	13.7	6.1	9.6
Overall mean	100.1	512.8	164.8	32.6	8.5	12.6	114.9	603.7	208.4	34.7	9.4	9.6

Table 13. Mean values for plant height (HT), biomass (BM), grain yield (GY), harvest index (HI), kernel weight (KW), and protein content (P) in F4 lines within crosses evaluated at Ruggs during the growing season 1992.

Genotype	Ruggs						East Farm					
	HT (cm)	BM (g)	GY (g)	HI (%)	KW (g)	P (%)	HT (cm)	BM (g)	GY (g)	HI (%)	KW (g)	P (%)
Wd-Neb 021//Cak-Mak	87.6	525.6	161.9	31.1	8.5	12.1	101.8	620.9	200.0	32.5	8.4	9.3
Wd-Neb 021//Parus	87.8	496.8	156.2	32.1	7.8	12.1	95.6	589.3	189.6	32.1	7.9	9.3
Wd-Neb 021//07690 Nic	97.9	550.2	163.7	30.5	7.5	12.7	113.9	650.8	225.3	34.9	8.9	9.5
Cak-Mak//Parus	106.3	451.9	149.6	33.5	9.2	12.1	124.1	586.7	216.2	36.8	9.7	10.2
Cak-Mak//07690 Nic	110.2	481.1	147.1	31.1	9.1	13.1	135.5	600.6	221.8	36.6	10.1	10.8
Parus //07690 Nic	114.1	461.5	155.9	33.5	9.2	13.7	129.9	589.8	210.5	35.8	10.5	10.4
LSD0.05	2.1	36.4	12.8	2.3	0.2	0.3	3.8	31.9	11.9	1.8	0.2	0.3
C.V	5.9	20.5	22.8	20.1	7.9	5.6	8.9	14.6	15.8	14.1	4.5	7.6
Overall means	100.6	494.5	155.7	31.9	8.5	12.6	116.8	606.3	210.6	34.8	9.2	9.9

### **Evaluation of Correlation Coefficients in F3 and F4 Lines**

One of the main objectives in breeding durum wheat is to maintain or increase protein content while improving grain yield. Because grain yield and protein content often cannot be assessed directly in early generations due to the influence of dominance and heterogeneity the direct measure is replaced by visual screening or by measuring a correlated trait.

This investigation was designated to identify possible selection criteria that are associated with grain yield, and protein content which can be used in early generation selection. Phenotypic, genotypic, and environmental correlations were computed on a per line mean basis between all possible pairs of traits except harvest index. These associations are provided in Tables 14a, and 14b, for F3 lines evaluated at Ruggs and East Farm, respectively. Associations among these traits for F4 are presented in Tables 15a, and 15b at both locations.

The genotypic correlation coefficients between grain yield and plant height, biomass, kernel weight, and protein content, tended to be larger in magnitude than their corresponding phenotypic correlations in F3 lines at both locations. The latter correlations were significant in both F3 and F4 lines at both locations. Other workers have also reported genotypic correlations that were larger than their respective phenotypic correlations between several traits in wheat (Kibite and Evans, 1984; Dyk and Baker, 1975). This indicates that these traits are either not genetically independent or that they are physiologically related as suggested by Sidwell et al. (1976). Phenotypic correlation coefficients were larger in F3 than in F4 lines at both locations. The largest and most consistent phenotypic and genotypic coefficients were observed between grain yield and biomass suggesting that grain yield may be enhanced by improving biomass. However, early generation selection for biomass may not be effective due to non-additive gene action controlling this trait (Study 1, Experiment 1).

Highly significant phenotypic correlations between grain yield and kernel weight were noted in both F3 and F4 lines at both locations. The positive genotypic and the inconsistent significance level of the environmental correlation coefficients between these traits suggest that kernel weight is the most desirable selection criterion to enhance grain yield. However, it would be necessary to investigate possible compensation interactions with other components of yields such as kernel number, and number of spikes per plant. Pinthus (1987) reported significant negative correlation coefficients between kernel weight and number of kernels in a study of two crosses of bread wheat. He attributed such associations to the compensation effects among these two traits. However, Pinthus and Millet (1978) showed that enough genetic variation in kernel weight is independent of number of kernels per spike to allow selection of lines potentially excelling in both traits in bread wheat.

A positive phenotypic association between protein content and plant height was noted in F3 lines but not in F4 lines at both locations. The genotypic correlation between these traits were moderate to low and inconsistent in sign. This may indicate that environmental effects or non additive genetic effects, or both, are acting on these traits in the same direction. It appears, however, that taller genotypes involving spring (07690 Nic) and facultative winter (Parus) cultivars were associated with higher protein content and kernel weight as compared to semi-dwarf genotypes involving winter cultivars Cak-Mak and Wd-Neb 021. Late maturity and delay in leaf senescence of tall lines involving the parental cultivar 07690 Nic may have allowed an extended period for protein translocation to the developing grain and as a result high protein mean values were obtained in these genotypes (Tables 12 and 13).

Negative genotypic correlations between grain yield and protein content were greater in magnitude than phenotypic coefficients at East Farm in both F3 and F4 lines. These associations were lower in magnitude than phenotypic correlations at Ruggs. This suggests

that environmental factors were apparently responsible for some of the inverse relationship between grain yield and protein content. O'Brien and Panozzo (1988) attributed the negative association between these traits to the potential manifestations of the seasonal conditions under which the crop was grown. The frequent negative genotypic correlation between grain yield and protein content is generally considered to be due to genetic causes suggesting either linkage or pleiotropy. This association was recognized to limit genetic advances in increasing both protein content and grain yield simultaneously (Guthrie et al. 1984; Löffler and Busch, 1982). However, increased grain yield and protein content was obtained (Schmidt et al. 1979) indicating that pleiotropy is not a factor in controlling the expression of these traits in bread wheat. In this study, it was generally observed that short stature lines produced moderate to high grain yield and were associated with low protein content than tall lines. Greater tillering ability and higher number of kernels per spike in semi-dwarf lines may have resulted in a negative association between grain yield and protein content. Anna et al. (1986), comparing tall and semi-dwarf lines from four crosses of durum wheat, found that semi-dwarf lines produced more kernels per spike and were associated with lower protein content than tall genotypes. They indicated that the limited amount of translocation of protein deposited in a greater number of kernels partly explained the negative association between grain yield and protein content. Moreover, environmental factors appeared to play a major role in the inverse relationship frequently observed between protein content and traits that were positively associated with grain yield. Nevertheless, results from this study suggest that selection for tall and heavier kernels genotypes can be attempted in early segregating populations to improve grain yield without a major decrease in protein content. However, a balance between plant height and lodging should be taken into consideration at this stage for the materials employed in this study.



Table 14a. Phenotypic ( $r_p$ ), genotypic ( $r_g$ ), and environmental ( $r_e$ ) correlations among five selected agronomic traits measured on per row plot basis, in F3 lines grown at Ruggs site (1991/92).

	Grain yield (g)			Protein content (%)		
	$r_p$	$r_g$	$r_e$	$r_p$	$r_g$	$r_e$
Plant height (cm)	0.164**	0.386	0.106	0.139*	0.123	-0.073
Biomass (g)	0.434**	0.998	0.611**	-0.516**	-0.046	-0.187**
Grain yield (g)	-----	-----	-----	-0.558**	-0.167	-0.114
Kernel weight (g)	0.418**	0.323	0.169*	-0.388**	-0.022	-0.221**
Protein content (%)	-0.558**	-0.167	-0.114	-----	-----	-----

\*,\*\* Significance at 0.05 and 0.01 probability levels respectively (n=120).

Table 14b. Phenotypic ( $r_p$ ), genotypic ( $r_g$ ), and environmental ( $r_e$ ) correlations among five selected agronomic traits measured on per row plot basis, in F3 lines grown at East Farm site (1991/92).

	Grain yield (g)			Protein content (%)		
	$r_p$	$r_g$	$r_e$	$r_p$	$r_g$	$r_e$
Plant height (cm)	0.273**	0.485	0.005	0.144**	0.144	0.042
Biomass (g)	0.835**	0.985	0.720**	-0.087	-0.268	0.187**
Grain yield (g)	-----	-----	-----	-0.151**	-0.316	-0.064
Kernel weight (g)	0.279**	0.503	0.309**	0.055	-0.326	-0.218**
Protein content (%)	-0.151**	-0.316	-0.064	-----	-----	-----

\*,\*\* Significance at 0.05 and 0.01 probability levels respectively (n=120).

Table 15a. Phenotypic ( $r_p$ ), genotypic ( $r_g$ ), and environmental ( $r_e$ ) correlations among five selected agronomic traits measured on per row plot basis, in F4 lines grown at Ruggs site (1991/92).

	Grain yield (g)			Protein content (%)		
	$r_p$	$r_g$	$r_e$	$r_p$	$r_g$	$r_e$
Plant height (cm)	0.246**	0.169	-0.051	0.016	-0.002	0.037
Biomass (g)	0.818**	0.990	0.459**	-0.445**	-0.097	-0.053
Grain yield (g)	-----	-----	-----	-0.475**	-0.231	-0.053
Kernel weight (g)	0.378**	0.332	0.189	-0.311**	-0.192	-0.191**
Protein content (%)	-0.475**	-0.231	-0.053	-----	-----	-----

\*,\*\* Significance at 0.05 and 0.01 probability levels respectively (n=120).

Table 15b. Phenotypic ( $r_p$ ), genotypic ( $r_g$ ), and environmental ( $r_e$ ) correlations among five selected agronomic traits measured on per row plot basis, in F4 lines grown at East Farm site (1991/92).

	Grain yield (g)			Protein content (%)		
	$r_p$	$r_g$	$r_e$	$r_p$	$r_g$	$r_e$
Plant height (cm)	0.459**	0.349	0.169*	0.003	-0.121	-0.027
Biomass (g)	0.855**	0.981	0.607**	-0.438**	-0.336	-0.051
Grain yield (g)	-----	-----	-----	-0.386**	-0.447	-0.023
Kernel weight (g)	0.352**	0.422	0.065	0.134*	-0.196	0.003
Protein content (%)	-0.386**	-0.447	-0.023	-----	-----	-----

\*,\*\* Significance at 0.05 and 0.01 probability levels respectively (n=120).

### **Predictions of F3 and F4 Progeny Rows**

Selection in early generation for grain yield and protein content is often practiced among F2 space planted progenies or in F3 populations grown in small plots with a limited number of replications. In this study, information was obtained on the effectiveness of single plant selection in F2 and F3 segregating populations for grain yield, protein content, plant height, biomass, harvest index, and kernel weight. Results of the simple associations between individual plant performance and row response are presented in Tables 16a and 16b for the F3 and F4 lines respectively. The largest associations between individual plant data and row performance were for plant height, kernel weight, and protein content in both F3 and F4 populations at both locations. This was true for model I involving individual plant performance and model II where individual plant data were adjusted for parental means plus unweighted progenitors plot deviations. However, associations using model I were higher for all traits measured. Although model II was recommended to increase prediction efficiency for low inherited traits such as grain yield and biomass in oats (Hill et al. 1991), this procedure appeared inadequate in predicting quantitatively inherited traits in the present investigation.

The significant correlation coefficients observed for plant height, kernel weight, and protein content further support the earlier discussed data that additive gene action controls the expression of these traits. Thus, using plant height and kernel weight as selection criteria in F2 or F3 space planted segregating populations might be an effective strategy to increase grain yield provided that compensation effects between other yield components are low. Significant association between individual plant performance and their corresponding row progenies for protein content indicated that direct selection for protein content as early as F2 plants is possible in this experimental material. It is noted however, that biomass, grain yield and

harvest index from spaced planted F3 populations were positively associated with F4 row performance, but their level of significance were inconsistent across locations. Negative associations were observed between F2 single plants and their corresponding F3 row progenies for these traits. Thus, visual assessment for biomass, grain yield and harvest index between F3 spaced plants can be recommended only if selection intensity is low enough to allow residual variability for further selection. Knott and Kumar (1975) found significant correlation coefficients between F3 and F5 lines for grain yield in two crosses of bread wheat. However, they reported that these correlations were too low to justify the efforts involved in early testing for grain yield. Van Oeveren (1992) recommended avoiding early generation selection even in F3 rows in self pollinated crops. He argued that inter-genotypic competition, small plot size and the high level of heterogeneity within plots affect the different genetic estimates and particularly the heritability leading to a low response to selection for grain yield. The relationships between grain yield and protein content from F3 and F4 row progenies with plant height, biomass, kernel weight, and harvest index from corresponding single plant are presented in Tables 17a and 17b respectively. Again, it was noted that adjusted individual plant observations (Model II) were not superior to those using unadjusted single plant data (Model I). Only kernel weight from single plant data were positively and consistently associated with both grain yield and protein content measured in F3 and F4 row progenies. Thus, kernel weight could be used as selection criterion in the F2 segregating populations to improve both grain yield and protein simultaneously.

Based on these results, it is clear that data pertaining to the performance in F2 and F3 spaced plants do not provide an adequate assessment of genetic potential for quantitative traits like grain yield, biomass and harvest index in subsequent generations grown in competitive stands. As pointed out by Islam et al. (1985b), the genetic factors determining the yield

potential in spaced plants are not identical with those operating in the presence of stress brought about by close spacing. This is because the yield of a plant grown under spaced planted conditions is not affected by the same limiting factors that operate at high density. The lack of linear relationships between single plant data with row progenies performance for biomass, grain yield, and harvest index may also be due in part to genotype x environment interactions and potential genetic heterogeneity in the segregating materials. These factors along with the preponderance of dominance effects in F2 segregating populations were recognized as principal factors affecting selection efficiency for quantitative traits (Wricke and Weber, 1986). Attempts to reduce the effects of these potential factors in predicting row progenies did not improve the relationship between single plant data in F2 and F3 and their corresponding row progenies.

Table 16a. Associations between F3 rows and spaced planted F2 data using unadjusted (Model I) and adjusted (Model II) grown at Ruggs and East Farm during 1992.

Traits	Ruggs		East Farm	
	F2 spaced planted vs F3 rows solid stand		F2 spaced planted vs F3 rows solid stand	
	Model I	Model II	Model I	Model II
Plant height (cm)	0.635**	0.576**	0.535***	0.615***
Biomass (g)	-0.155	-0.176	-0.026	-0.017
Grain yield (g)	-0.189*	-0.199*	-0.047	-0.080
Harvest index (%)	0.023	0.088	-0.17	-0.078
Kernel weight (g)	0.383**	0.369**	0.261*	0.293***
Protein content (%)	0.107	-0.015	0.293***	0.177*

\*\*, \* significant at 0.01 and 0.05 probability levels respectively  
n=120 for all observations.

Table 16b. Associations between F4 rows and spaced planted F3 data using unadjusted (Model I) and adjusted (Model II) grown at Ruggs and East Farm during 1992.

Traits	Ruggs		East Farm	
	F3 spaced planted vs F4 rows solid stand		F3 spaced planted vs F4 rows solid stand	
	Model I	Model II	Model I	Model II
Plant height (cm)	0.569**	0.520 <sup>***</sup>	0.611 <sup>***</sup>	0.544 <sup>***</sup>
Biomass (g)	0.130	0.007	0.200*	0.189*
Grain yield (g)	0.124	0.026	0.151	0.130
Harvest index (%)	0.211**	0.159	0.178*	0.162
Kernel weight (g)	0.516**	0.380 <sup>***</sup>	0.535 <sup>***</sup>	0.515 <sup>***</sup>
Protein content (%)	0.410**	0.355 <sup>***</sup>	0.273 <sup>***</sup>	0.323 <sup>***</sup>

\*\*, \* significant at 0.01 and 0.05 probability levels respectively  
n=120 for all observations.

Table 17a. Relationships between grain yield (GY) and protein content (P) measured on a per row plot basis in F3 lines with plant height, biomass, harvest index, and kernel weight from individual F2 space planted using adjusted (Model I) and unadjusted data (Model II).

Traits	Ruggs				East Farm			
	Model I		Model II		Model I		Model II	
	GY (g)	P (%)	GY (g)	P (%)	GY (g)	P (%)	GY (g)	P
Plant height (cm)	-0.070	0.388**	-0.188**	0.523**	0.285**	0.166	0.335**	0.084
Biomass (g)	0.247**	0.163	-0.246**	0.210*	0.063	0.033	0.017	0.141
Harvest index (%)	0.097	-0.133	0.026	-0.125	-0.167	0.023	-0.139	0.006
Kernel weight (g)	0.248**	0.175	0.231**	0.146	0.137	0.144	0.283**	0.211**

\*,\*\* significant at 0.01 and 0.05 probability levels respectively  
n=120 for all observations



Table 17b. Relationships between grain yield (GY) and protein content (P) measured on a per row plot basis in F4 lines with plant height, biomass, harvest index, and kernel weight from individual F3 spaced planted using adjusted (Model I) and unadjusted data (Model II).

Traits	Ruggs				East Farm			
	Model I		Model II		Model I		Model II	
	GY (g)	P (%)	GY (g)	P (%)	GY (g)	P (%)	GY (g)	P (%)
Plant height (cm)	-0.138	0.322**	-0.067	0.480**	0.165	0.322**	0.148	0.258**
Biomass (g)	0.033	0.037	0.017	0.212*	0.197*	0.058	0.205*	0.156
Harvest index (%)	-0.015	0.074	-0.036	-0.121	-0.100	0.141	-0.132	0.128
Kernel weight (g)	0.177*	0.342**	0.331**	0.259**	0.231**	0.392**	0.265**	0.462**

\*,\*\* significant at 0.01 and 0.05 probability levels respectively  
n=120 for all observations

### **Heritability Estimates for Kernel Weight, Grain Yield and Protein Content**

Broad sense heritability reflects the total amount of genetic variability for a given trait. This includes genes which are additive and non additive in their action. In the F3 and F4, with the loss of heterozygosity, it would be expected that the nature of gene action would be largely additive. Nevertheless, non-fixable genetic variation is likely to distort but not invalidate estimates. Heritability estimates within crosses for kernel weight, grain yield and protein content are given in Table 18. These estimates were generally lower in magnitude in the F3 than those observed in the F4 lines for the three traits. This could be due to the fact that F4 lines are more homogeneous and therefore are associated with a smaller error variance. It appears also that adverse growing conditions at the Ruggs site reduced the heritability estimates. These effects were more pronounced in F3 than in F4 lines. Heritability estimates were relatively higher for kernel weight than for grain yield and protein content in both F3 and F4 lines. This is expected due to the magnitude of additive effects controlling kernel weight. Similar results were reported by Anna et al.(1986) and Cantrell and Haro-Arias (1986) in durum wheat. This may indicate that kernel weight is sufficiently heritable to permit some genetic advance through selection for this trait in F2 populations.

Heritability estimates for each of the three traits varied from cross to cross and over environments. Higher heritability estimates at both locations were noted for kernel weight in crosses Parus//07690 Nic in F3 and Cak-Mak//Parus in F4 lines, respectively. Heritability estimates for grain yield ranged from low (0.14) to high (0.88) depending on the cross, generation and environment. However, the highest and the most consistent estimates were observed for the cross Wd-Neb021//07690 Nic in both F3 and F4 lines at both experimental sites. Greater heritability estimates for protein content were detected in the cross Wd-Neb

021//Parus in both F3 and F4 lines. These results are in agreement with GCA where the parental cultivars 07690 Nic, Parus, and Cak-Mak were found to be associated with positive  $g_i$  for kernel weight, protein content, and grain yield respectively.

Since heritability estimates depend on the genotypic variance, greater response to selection can be expected in uniform environments. Ceccarelli et al. (1991) noted that high heritability estimates in stress free environments have been used as an argument for selecting only in favorable growing conditions even when the target environment is stress prone. O'Brien et al. (1978) reported that although response to selection in bread wheat will be more efficient in populations with large genetic variance, the highest yielding lines may be derived from populations with less genetic variance but having large initial mean yield. In this study, greater heritability estimates, genotypic variability, and higher mean values were noted at East Farm for most traits suggesting that this site is particularly suitable to select for kernel weight, and protein content in the F2 generation. However, the most desirable approach to select for grain yield and other attributes should include both stress and non-stress environments. By using information from both locations, it is possible to maintain stress tolerant genotypes that may be lost if early selection is carried out only in favorable environments. It is noted however, that the effectiveness of selection for grain yield and protein content in early generation depends not only on the heritability and genetic variance of these traits, but also on any unfavorable correlated responses (Fischer et al. 1989). Ketata et al. (1976) pointed out that reporting both genetic advance and heritability estimates is more informative in genetic and breeding studies than showing either alone. Therefore estimates of direct and correlated selection responses could provide some indication of the potential cross where superior lines for grain yield and protein content are most likely.

Table 18. Within cross broad sense heritability estimates based on variance components for kernel weight, grain yield, and protein content in F3 and F4 lines grown on the East Farm and Ruggs during 1992 growing season.

Cross	Location	F3 Lines			F4 Lines		
		Kernel weight (g)	Grain yield (g)	Protein content (%)	Kernel weight (g)	Grain yield (g)	Protein content (%)
Wd-Neb 021 // Cak-Mak	Ruggs	0.51	0.14	0.18	0.68	0.64	0.63
	East Farm	0.62	0.45	0.56	0.85	0.72	0.93
Wd-Neb 021 // Parus	Ruggs	0.48	0.31	0.56	0.72	0.24	0.21
	East Farm	0.61	0.48	0.54	0.76	0.45	0.60
Wd-Neb 021 // 07690 Nic	Ruggs	0.42	0.39	0.56	0.56	0.60	0.38
	East Farm	0.90	0.78	0.55	0.87	0.86	0.60
Cak-Mak // Parus	Ruggs	0.68	0.38	0.53	0.74	0.36	0.50
	East Farm	0.74	0.43	0.68	0.92	0.72	0.68
Cak-Mak // 07690 Nic	Ruggs	0.65	0.16	0.43	0.50	0.42	0.56
	East Farm	0.58	0.52	0.40	0.92	0.83	0.80
Parus // 07690 Nic	Ruggs	0.68	0.36	0.39	0.49	0.27	0.69
	East Farm	0.80	0.62	0.87	0.91	0.88	0.90

n=20

### **Responses to Selection for Kernel Weight, Grain Yield, and Protein Content**

Estimates of direct and correlated responses to selection for kernel weight, grain yield, and protein content are provided in Tables 19a and 19b for F3 and F4 lines, respectively. Direct responses in both F3 and F4 lines to selection were greater in magnitude than correlated responses for each of the three traits. However, these estimates varied from cross to cross and between environments. Larger responses to selection were noted at East Farm than those obtained at Ruggs for all three traits. The largest direct response to selection for kernel weight was noted in the cross Wd-Neb021//07690 Nic in the F3 and Wd-Neb 021//Cak-Mak in the F4 lines. This indicates that 07690 Nic and Cak-Mak had transmitted their additive genetic effects to these progenies. Low correlated responses for grain yield were noted in most crosses except Wd-Neb021//07690 Nic and Cak-Mak//Parus in F3 and F4 lines, respectively. This lack of correspondence between direct response to selection for kernel weight and the corresponding correlated responses for grain yield indicates that increased grain yield may be not the result of increased kernel weight alone. Increased number of kernels per spike associated with a lower kernel weight may have contributed to the low correlated responses for grain yield in some lines particularly those from the parental cultivars Wd-Neb 021. Higher, kernel weight determined grain yield mostly in lines involving the parental cultivar Cak-Mak in combination with either 07690 Nic and Parus.

Direct selection for kernel weight caused substantial decreases in protein content in all crosses averaging 0.38% and 0.25% in F3 and F4 lines, respectively. These results are contrary to predictions of row progenies where kernel weight per plant basis was found to be positively associated with protein content measured on a per row basis. This may be due to several causes. First, correlation coefficients between individual plant and row data were

estimated by pooling observations over lines. Second, it might be argued that a single sample of 200 kernels from each line may not be representative of an F2 or F3 parental plant.

Estimates of direct response to selection for grain yield averaged 23.82 g and 34.23 g in F3 and F4 lines, respectively. However, higher mean values at the two environments were noted in the cross Wd-Neb021//07690 Nic. This, again, is in agreement with the results from Study 1 Experiment 1, where selection 07690 Nic was found to have the largest  $g_i$  effects for grain yield. Direct selection for grain yield was associated with positive but low correlated responses for kernel weight and negative correlated responses for protein content in all crosses in both F3 and F4 lines. The correlated responses of protein content were lower in F3 than in F4 lines averaging -0.17% and -0.27%, respectively. Although differential correlated responses for protein content were observed in the six crosses, comparable mean responses at both locations were noted in F3 but not in F4 lines. This result indicates that gain from selection for grain yield may not affect the response of protein content in F3 generation. However, in the present study non additive gene action was preponderant in the inheritance of grain yield, while additive gene action was largely involved in the expression of protein content. Moreover, these traits appeared to be controlled by independent factors in this material. Hence, sufficient variation should exist for both grain yield and protein content by intensively selecting for protein content in the F2 and F3 generations prior to yield testing.

Expected response to selection for protein content over the two environments and six crosses yielded 0.51% and 0.68% in F3 and F4 lines respectively. These direct responses were associated with an average decrease of 9.31 g and 14.53 g in grain yield in F3 and F4 lines, respectively. The relatively small gain in F4 over F3 lines may not be sufficient to justify delayed selection for protein content. This supports the argument that selection in F2 populations for protein content may not result in a major decrease in grain yield in later

generations. The highest direct responses to selection for protein content were noted in the cross Wd-Neb 021//07690 Nic and Parus//07690 Nic in F3 and F4 lines, respectively. This expected since the parental cultivars Parus and 07690 Nic were identified as the best combiners for protein content (Study 1 Experiment 1).

Table 19a. Expected response (R) and correlated responses (CR) for kernel weight (KW), grain yield (GY), and protein content (P) for F3 lines (within each of the six crosses) grown at Ruggs and East Farm during 1992.

Cross	Location	$R_{(KW)}$ (g)	$CR_{(KW,GY)}$ (g)	$CR_{(KW,P)}$ (%)	$CR_{(GY,KW)}$ (g)	$R_{(GY)}$ (g)	$CR_{(GY,P)}$ (%)	$CR_{(P,KW)}$ (g)	$CR_{(P,GY)}$ (g)	$R_{(P)}$ (%)
Wd-Neb 021 // Cak-Mak	Ruggs	<b>0.37</b>	4.13	-0.65	0.04	<b>10.81</b>	-0.30	-0.02	-9.69	<b>0.44</b>
	East Farm	<b>0.52</b>	28.77	-0.02	0.42	<b>25.53</b>	-0.08	-0.20	-4.56	<b>0.53</b>
Wd-Neb 021 // Parus	Ruggs	<b>0.31</b>	2.56	-0.26	0.03	<b>17.14</b>	-0.12	-0.22	-8.29	<b>0.43</b>
	East Farm	<b>0.45</b>	0.32	-0.68	0.01	<b>14.06</b>	-0.11	-0.41	-2.54	<b>0.66</b>
Wd-Neb 021 // 07690 Nic	Ruggs	<b>0.40</b>	14.22	-0.37	0.34	<b>15.39</b>	-0.16	-0.41	-7.56	<b>0.48</b>
	East Farm	<b>0.94</b>	18.95	-0.90	0.28	<b>55.12</b>	-0.43	-0.53	-17.13	<b>0.97</b>
Cak-Mak // Parus	Ruggs	<b>0.53</b>	3.06	-0.24	0.04	<b>25.41</b>	-0.07	-0.27	-6.90	<b>0.37</b>
	East Farm	<b>0.79</b>	24.28	-0.71	0.37	<b>30.34</b>	-0.31	-0.74	-21.75	<b>0.69</b>
Cak-Mak // 07690 Nic	Ruggs	<b>0.47</b>	2.50	-0.07	0.02	<b>13.77</b>	-0.06	-0.12	-7.81	<b>0.18</b>
	East Farm	<b>0.45</b>	15.84	-0.01	0.27	<b>23.44</b>	-0.16	-0.01	-12.64	<b>0.38</b>
Parus // 07690 Nic	Ruggs	<b>0.54</b>	6.01	-0.49	0.07	<b>24.31</b>	-0.19	-0.21	-11.39	<b>0.43</b>
	East Farm	<b>0.72</b>	16.81	-0.16	0.31	<b>30.20</b>	-0.02	-0.35	-1.43	<b>0.58</b>
Means at Ruggs		<b>0.44</b>	5.41	-0.35	0.09	<b>17.81</b>	-0.15	-0.21	-8.61	<b>0.39</b>
Means at East Farm		<b>0.65</b>	17.50	-0.41	0.28	<b>29.84</b>	-0.19	-0.37	-10.01	<b>0.64</b>
Overall Mean		<b>0.54</b>	11.50	-0.38	0.18	<b>23.82</b>	-0.17	-0.29	-9.31	<b>0.51</b>

n=20



Table 19b. Expected response (R) and correlated responses (CR) for kernel weight (KW), grain yield (GY), and protein content (P) for F4 lines (within each of the six crosses) grown at Ruggs and East Farm during 1992.

Cross	Location	$R_{(KW)}$ (g)	$CR_{(KW,GY)}$ (g)	$CR_{(KW,P)}$ (%)	$CR_{(GY,KW)}$ (g)	$R_{(GY)}$ (g)	$CR_{(GY,P)}$ (%)	$CR_{(P,KW)}$ (g)	$CR_{(P,GY)}$ (g)	$R_{(P)}$ (%)
Wd-Neb 021 // Cak-Mak	Ruggs	<b>0.77</b>	10.20	-0.11	0.28	<b>26.05</b>	-0.13	-0.12	-4.92	<b>0.66</b>
	East Farm	<b>0.81</b>	2.15	-0.53	0.05	<b>28.26</b>	-0.14	-0.43	-4.82	<b>1.09</b>
Wd-Neb 021 // Parus	Ruggs	<b>0.21</b>	3.18	-0.02	0.02	<b>16.94</b>	-0.01	-0.01	-0.32	<b>0.14</b>
	East Farm	<b>0.30</b>	16.18	-0.37	0.08	<b>36.61</b>	-0.53	-0.13	-37.63	<b>0.69</b>
Wd-Neb 021 // 07690 Nic	Ruggs	<b>0.48</b>	4.23	-0.18	0.08	<b>25.78</b>	-0.37	-0.16	-16.50	<b>0.57</b>
	East Farm	<b>0.90</b>	27.21	-0.23	0.39	<b>62.91</b>	-0.57	-0.23	-41.40	<b>0.39</b>
Cak-Mak // Parus	Ruggs	<b>0.42</b>	27.29	-0.03	0.19	<b>28.84</b>	-0.03	-0.02	-3.40	<b>0.31</b>
	East Farm	<b>0.88</b>	31.64	-0.44	0.45	<b>48.26</b>	-0.02	-0.35	-0.94	<b>0.82</b>
Cak-Mak // 07690 Nic	Ruggs	<b>0.42</b>	1.72	-0.06	0.04	<b>15.79</b>	-0.24	-0.06	-10.94	<b>0.46</b>
	East Farm	<b>1.12</b>	15.01	-0.25	0.31	<b>48.65</b>	-0.28	-0.25	-13.95	<b>0.96</b>
Parus // 07690 Nic	Ruggs	<b>0.46</b>	9.03	-0.21	0.17	<b>13.67</b>	0.00	-0.19	-0.22	<b>0.72</b>
	East Farm	<b>0.77</b>	45.55	-0.58	0.57	<b>58.94</b>	-0.89	-0.32	-39.34	<b>1.37</b>
Means at Ruggs		<b>0.46</b>	9.30	-0.10	0.13	<b>21.18</b>	-0.13	-0.10	-6.10	<b>0.48</b>
Means at East Farm		<b>0.80</b>	22.96	-0.40	0.31	<b>47.30</b>	-0.41	-0.29	-23.01	<b>0.89</b>
Overall Means		<b>0.63</b>	16.1	-0.25	0.22	<b>34.23</b>	-0.27	-0.19	-14.53	<b>0.68</b>

n=20

## SUMMARY AND CONCLUSIONS

The objectives of this investigation were to provide information on the nature of inheritance of grain yield, protein content, and other selected agronomic traits; to evaluate the possible associations between these traits, and to determine the effectiveness of single plant selection under space planting on the subsequent performance in a solid seeded conditions. Three winter and one spring durum cultivars representing wide variation for the traits of interest were crossed in a diallel fashion. Data were collected on an individual plant basis for plant height, number of spikes, number of kernels per spike, biomass, grain yield, harvest index, kernel weight, and protein content. Data from F1's and parental cultivars were examined using combining ability analysis to determine the nature of gene action controlling the expression of the traits measured. Mean generation analysis within each cross was also carried out using data from parents, F1, F2, and F3 grown under spaced planted conditions at two environmentally diverse locations.

The effectiveness of individual plant selections from early segregating populations was evaluated using 20 F2 and 20 F3 plants from each of the six crosses. A random sample of 600 seeds from each F2 and F3 spaced individual plants was used to establish progeny rows so that each row could be traced back to an individual plant. The selected materials were grown in three replications at the two sites. Phenotypic, genotypic, and environmental correlations between plant height, biomass, grain yield, harvest index, kernel weight, and protein content were determined for F3 and F4 lines at each location. The reliability of single plant selection was evaluated using correlation coefficients between data from selected F2 and F3 plants and their row progenies using unadjusted (Model I) and adjusted (Model II) single plant data. Within cross heritability estimates using components of variances were computed for kernel

weight, grain yield and protein content in both F3 and F4 lines. Direct and correlated responses to selection for these traits were estimated on a per cross basis within each location.

Based on results from this investigation, the following conclusions are drawn:

1. Significant differences among entries were obtained for all traits measured in Experiment 1. From the mean square values of the five generations (Experiment 2 and 3), genetic variability was greatest for plant height, kernel weight, and protein content in most crosses at both locations. Differential responses within each location for number of spikes, biomass, grain yield, and harvest index were obtained. At East Farm, the five generations from the crosses Wd-Neb 021// 07690 Nic and Parus//07690 Nic differed significantly for most traits.
2. Significant GCA and SCA estimates were obtained for most of the traits. Additive gene action was the major contributing factor in controlling the expression of plant height, kernel weight, and protein content suggesting that early generation selection for these traits could be effective. Specific combining ability was predominant in controlling number of spikes, biomass, kernel number, grain yield, and harvest index suggesting that non additive gene action was important in controlling these traits. Early generation selection for these traits would be therefore, ineffective.
3. The cultivar 07690 Nic has the highest  $g_i$  effects for plant height and number of spikes per plant. Parus, and Cak-Mak had the highest  $g_i$  effects for protein content and kernel weight, respectively. No significant  $g_i$  effects were found for biomass, grain yield, harvest index and number of kernels per spike in all parent. The lack of agreement between  $g_i$  effects and parental mean values suggests that the parental performance per se may not result in the best possible cross combination for these traits.

4. The best cross combinations involving parents with high  $g_i$  effects for plant height, number of spikes per plant, kernel weight, and protein content were those observed between the spring selection 07690 Nic with the winter cultivars Parus, and Cak-Mak. High mean values and significant  $s_{ij}$  effects were noted in these crosses for biomass, grain yield, harvest index, number of kernels per spikes suggesting that the parental cultivars contributed in non-additive manner to these traits. The cross Parus//07690 Nic had the highest mean values and  $s_{ij}$  effects for most traits.
5. Estimates of genetic effects using mean generation analysis were genotype and environment specific. No significant estimates of genetic effects were found for biomass, number of spikes, and grain yield in the five generations in all crosses at both locations suggesting that large genotype x environment interactions were associated with these estimates.
6. Most of the genetic variability was found in crosses between Cak-Mak, Parus, and 07690 Nic for plant height, kernel weight, harvest index, and protein content. Partial agreement between  $g_i$  effects from Experiment 1 and estimates of genetic effects from Experiment 3 was noted in winter x spring crosses for these traits. Consistent additive genetic effects from mean generation analysis controlling the expression of protein content in the cross Parus//07690 Nic at both locations is in agreement with estimates of  $g_i$  effects.
7. Associations between agronomic traits indicated that grain yield was positively correlated with plant height, biomass, and kernel weight. These associations were in general greater in F4 than in F3 lines. Protein content was negatively associated with yield. Dilution of protein due to a large number of kernels per spike and genotype x environment interactions were responsible for this inverse relationship.

8. Significant associations between single plant data and progeny rows were observed for plant height, kernel weight, and protein content confirming that selection in F<sub>2</sub> segregating populations for these traits is possible. Adjustment of single plant data (Model II) did not improve the prediction of row progenies for biomass, grain yield, and harvest index. Therefore selection for these traits should be delayed until F<sub>4</sub> or later generations and assessed in solid seeded conditions.
9. The highest mean values for all traits were noted in crosses involving 07690 Nic at both locations in F<sub>3</sub> and F<sub>4</sub> lines. Heritability estimates for kernel weight, grain yield and protein content in F<sub>3</sub> and F<sub>4</sub> lines were greater at East Farm than at Ruggs. These data indicated that an environment conducive to higher mean values and greater variability should be considered in early generation selection for kernel weight and protein content. The highest heritability estimates for these traits were obtained from the crosses Wd-Neb021//07690 Nic and Parus//07690 Nic in F<sub>3</sub> and F<sub>4</sub> lines at this site. This was in agreement with estimates of genetic effects.
10. Direct selection for kernel weight was associated with increase in grain yield and did not cause a major reduction in protein content in either F<sub>3</sub> and F<sub>4</sub> lines. Estimates of gene action, predictions of progeny rows, heritability estimates, and responses to selections indicated that selection for kernel weight and protein content in F<sub>2</sub> prior to yield testing could be effective in improving both grain yield and protein content.
11. In this study, winter x spring crosses offered additional sources of genetic variability for most of the traits. Additive gene action played a major role for plant height, kernel weight, and protein content in the winter x spring crosses. Multilocation testing should be considered to reduce the effects of the differential responses to the environment which appears to influence both additive and non additive gene action.

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## **APPENDIX**

Table 1. Detailed description of the four parental cultivars included in the study.

Accessions #	Pedigree	Origin	Growth habit	Agronomic characteristics
3880136	Wd-Neb 021	Nebraska	Winter	Semi-dwarf (99 cm), white chaff and awns, wide and short flag leaves, partial fertile spikes, narrow culm, medium yielding, low protein content.
6870703	Cak-Mak 79	Eskisehir, Turkey	Facultative winter	Semi-dwarf (108 cm), white chaff and awns, narrow flag leaves, high kernel weight, susceptible to yellow berry, high spike fertility, high tiller number, high grain yield, low protein content.
3880181	Parus	Ukraine	Winter	Semi-dwarf(98 cm), brown glumes and awns, highly fertile spikes, intermediate grain yield, high protein content.
4880003	07690 Nic	North Dakota	Spring	Tall (127 cm), susceptible to lodging, elongated flag leaves, high spike fertility, plump kernels, high yield, intermediate protein content.

Table 2. Weather summary of the 1989/90 crop year At East Farm.

Month	Maximum temperature (°C)	Minimum temperature (°C)	Monthly mean temperature (°C)	Monthly precipitations (mm)
September	34	2	18	15
October	25	-5	11	66
November	18	-3	9	98
December	15	-2	6	77
January	16	3	6	237
February	18	-8	5	145
March	21	-2	9	55
April	26	0	12	56
May	29	0	12	36
June	35	7	16	38
July	37	7	20	11
August	38	6	20	43



Table 3. Weather summary of the 1991/92 crop year At East Farm.

Month	Maximum temperature (°C)	Minimum temperature (°C)	Monthly mean temperature (°C)	Monthly precipitations (mm)
September	28	10	19	0
October	20	5	-15	5
November	12	5	9	65
December	8	2	5	130
January	16	-4	6	115
February	20	-3	9	115
March	21	0	10	26
April	24	1	12	104
May	32	8	16	0
June	39	5	19	30
July	37	10	20	30
August	39	7	20	11

Table 4. Weather summary of the 1990/91 crop year At Ruggs.

Month	Maximum temperature (°C)	Minimum temperature (°C)	Monthly mean temperature (°C)	Monthly precipitations (mm)
September	30	7	19	0
October	18	2	10	35
November	13	2	7	4
December	2	-10	-4	30
January	4	-5	-1	29
February	13	1	7	22
March	11	-1	5	3
April	17	2	9	26
May	19	5	12	120
June	23	8	15	0
July	31	10	21	4
August	33	12	22	6

Table 5. Weather summary of the 1991/92 crop year At Ruggs.

Month	Maximum temperature (°C)	Minimum temperature (°C)	Monthly mean temperature (°C)	Monthly precipitations (mm)
September	28	6	17	1
October	19	1	10	23
November	9	1	5	106
December	6	-1	2	25
January	7	0	4	24
February	11	1	6	34
March	15	0	8	22
April	18	4	11	33
May	25	5	15	5
June	30	10	20	23
July	30	12	21	44
August	31	11	21	20

Table 6. Mean squares for plant height (HT), number of spike (SP), biomass (BM), grain yield (GY), harvest index (HI), kernel weight (KW), and protein content (P) in the five generations (parents, F1, F2 and F3) evaluated at Ruggs during 1991.

Cross	Source	D.f	HT	SP	BM	GY	HI	KW	P
Wd-Neb021// Cak-Mak	Rep	2	119.04	415.22	15918.26	2193.69	35.61	0.42	0.07
	Gen	4	8.18 <sup>ns</sup>	33.03*	1002.39*	74.77 <sup>ns</sup>	35.04*	1.42 <sup>***</sup>	2.55 <sup>***</sup>
	Error	8	9.83	1.58	169.34	30.73	6.84	0.20	0.32
Wd-Neb021// Parus	Rep	2	63.16	289.43	12701.45	1626.70	7.27	0.11	0.27
	Gen	4	45.12*	2.82 <sup>***</sup>	392.77 <sup>***</sup>	49.33 <sup>***</sup>	6.61 <sup>ns</sup>	0.80*	2.25 <sup>***</sup>
	Error	8	9.93	1.10	59.14	6.32	5.25	0.08	0.25
Wd-Neb021// 07690 Nic	Rep	2	115.11	630.32	16100.27	2068.61	14.79	0.30	0.44
	Gen	4	314.98 <sup>***</sup>	4.83 <sup>ns</sup>	418.92*	71.43 <sup>***</sup>	3.66 <sup>ns</sup>	0.55 <sup>***</sup>	0.56 <sup>ns</sup>
	Error	8	16.23	3.96	110.1	6.76	3.94	0.05	0.20
Cak-Mak // Parus	Rep	2	76.05	378.71	14447.6	2275.41	10.88	0.48	0.22
	Gen	4	240.45 <sup>***</sup>	5.44 <sup>ns</sup>	461.65 <sup>ns</sup>	45.05 <sup>ns</sup>	18.79 <sup>ns</sup>	0.30*	0.85 <sup>***</sup>
	Error	8	16.66	2.43	219.49	43.04	7.71	0.05	0.04
Cak-Mak // 07690 Nic	Rep	2	154.32	477.20	18998.2	2335.8	15.08	0.53	0.08
	Gen	4	255.45 <sup>***</sup>	14.42*	224.44 <sup>ns</sup>	54.01 <sup>ns</sup>	15.65 <sup>ns</sup>	0.21 <sup>ns</sup>	0.56*
	Error	8	20.83	2.52	101.75	28.35	8.99	0.09	0.09
Parus // 07690 Nic	Rep	2	61.45	346.96	14799.94	1790.51	3.59	0.39	0.04
	Gen	4	536.29*	9.81*	114.31 <sup>ns</sup>	6.08 <sup>ns</sup>	7.06*	2.47 <sup>***</sup>	0.35*
	Error	8	46.11	1.47	61.23	12.23	2.38	0.05	0.07

\*, \*\*, significantly different from zero at 5% and 1% probability level respectively.  
ns, not significant at 5% probability level.

Table 7. Mean squares for plant height (HT), number of spike (SP), biomass (BM), grain yield (GY), harvest index (HI), kernel weight (KW), and protein content (P) in the five generations (parents, F1, F2 and F3) evaluated at East Farm during 1992.

Cross	Source	D.f	HT (cm)	SP	BM (g)	GY (g)	HI (%)	KW (g)	P (%)
Wd-Neb021//Cak-Mak	Rep	2	56.84	82.11	7134.81	1094.10	24.31	0.51	0.25
	Gen	4	23.20*	2.08*	196.40 <sup>***</sup>	10.59*	2.63 <sup>ns</sup>	0.94 <sup>ns</sup>	1.54 <sup>ns</sup>
	Error	8	3.84	0.59	17.73	2.31	1.49	0.34	0.52
Wd-Neb021//Parus	Rep	2	74.65	65.96	6448.89	112.11	20.19	1.00	0.01
	Gen	4	59.64 <sup>***</sup>	1.59 <sup>ns</sup>	93.93 <sup>ns</sup>	16.11*	2.92 <sup>ns</sup>	1.56*	3.94 <sup>***</sup>
	Error	8	5.20	1.19	51.01	4.87	3.19	0.44	0.54
Wd-Neb021 // 07690 Nic	Rep	2	38.04	73.36	7846.26	1187.76	22.69	0.35	0.49
	Gen	4	307.27*	1.44 <sup>ns</sup>	136.56*	44.66*	12.23 <sup>***</sup>	2.52 <sup>***</sup>	11.69 <sup>***</sup>
	Error	8	45.28	0.38	34.81	8.03	1.01	0.31	0.16
Cak-Mak // Parus	Rep	2	48.07	73.35	4879.42	862.42	37.74	1.98	0.09
	Gen	4	15.73*	8.63*	314.08 <sup>***</sup>	30.43 <sup>***</sup>	10.53 <sup>ns</sup>	0.12 <sup>ns</sup>	1.72*
	Error	8	2.37	1.80	24.76	4.02	3.82	0.61	0.37
Cak-Mak // 07690 Nic	Rep	2	24.40	76.68	6983.56	1259.23	69.70	1.01	0.01
	Gen	4	313.26*	2.52*	64.94 <sup>ns</sup>	9.32 <sup>ns</sup>	5.68 <sup>ns</sup>	0.78 <sup>ns</sup>	8.75 <sup>***</sup>
	Error	8	25.10	0.86	35.97	4.69	2.64	0.43	0.10
Parus // 07690 Nic	Rep	2	30.81	44.41	5063.24	852.78	28.58	2.72	0.22
	Gen	4	387.65 <sup>***</sup>	4.97*	318.69*	49.52 <sup>***</sup>	8.22 <sup>ns</sup>	3.89*	7.90 <sup>***</sup>
	Error	8	46.24	0.90	46.44	4.99	4.26	0.83	0.51

\*,\*\*, significantly different from zero at 5% and 1% probability level respectively.

ns, not significant at 5% probability level.

Table 8. Levels of significance of the C, D and joint (J) scaling tests for plant height (HT), number of spike (SP), biomass (BM), grain yield (GY), harvest index (HI), kernel weight (KW), and protein content (P) in six durum wheat crosses evaluated at Ruggs during 1991 growing season.

Cross	Tests	Ruggs 1991						
		HT	SP	BM	GY	HI	KW	P
Wd-Neb021//Cak-Mak	C	ns	ns	ns	ns	**	ns	ns
	D	ns	ns	ns	ns	ns	*	**
	J	ns	ns	ns	ns	**	*	**
Wd-Neb021//Parus	C	ns	ns	ns	ns	ns	ns	*
	D	ns	ns	ns	ns	ns	**	ns
	J	ns	ns	ns	ns	ns	**	*
Wd-Neb021//07690 Nic	C	ns	ns	ns	ns	ns	ns	ns
	D	ns	ns	ns	ns	ns	ns	ns
	J	ns	ns	ns	ns	ns	ns	ns
Cak-Mak//Parus	C	ns	ns	ns	ns	ns	ns	ns
	D	*	ns	ns	ns	**	ns	ns
	J	*	ns	ns	ns	*	ns	ns
Cak-Mak//07690 Nic	C	ns	ns	ns	ns	ns	ns	**
	D	ns	ns	ns	ns	ns	ns	**
	J	ns	ns	ns	ns	ns	ns	**
Parus//07690	C	ns	ns	ns	ns	ns	*	*
	D	ns	ns	ns	ns	ns	**	*
	J	ns	ns	ns	ns	ns	**	ns

\*, \*\*, significantly different from zero at 0.05 and 0.01 probability levels respectively; ns, not significant at 0.05.

Table 9. Levels of significance of the C, D and joint (J) scaling tests for plant height (HT), number of spike (SP), biomass (BM), grain yield (GY), harvest index (HI), kernel weight (KW), and protein content (P) in six durum wheat crosses evaluated East Farm during 1992 growing season.

Cross	Tests	East Farm 1992						
		HT	SP	BM	GY	HI	KW	P
Wd-Neb021//Cak-Mak	C	*	ns	ns	ns	ns	ns	ns
	D	ns	ns	ns	ns	ns	ns	**
	J	ns	ns	ns	ns	ns	ns	**
Wd-Neb021//Parus	C	ns	ns	ns	ns	ns	ns	**
	D	ns	ns	ns	ns	ns	**	ns
	J	ns	ns	ns	ns	ns	**	*
Wd-Neb021//07690 Nic	C	**	ns	ns	ns	**	ns	ns
	D	ns	ns	ns	ns	ns	ns	*
	J	**	ns	ns	ns	**	ns	ns
Cak-Mak//Parus	C	ns	ns	ns	ns	ns	ns	**
	D	ns	ns	ns	ns	ns	ns	*
	J	ns	ns	ns	ns	ns	ns	**
Cak-Mak//07690 Nic	C	ns	ns	ns	ns	ns	ns	ns
	D	*	ns	ns	ns	ns	ns	**
	J	**	ns	ns	ns	ns	ns	**
Parus//07690	C	ns	ns	ns	ns	ns	ns	ns
	D	ns	ns	ns	ns	ns	ns	ns
	J	ns	ns	ns	ns	ns	ns	ns

\*,\*\*, significantly different from zero at 0.05 and 0.01 probability levels respectively; ns, not significant at 0.05.

Table 10. Combined analysis of variance for plant height (HT), biomass (BM), grain yield (GY), harvest index (HI), kernel weight (KW), and protein content (P) of F3 lines evaluated at Ruggs and East Farm during 1992 growing season.

Source	D.f	HT	BM	GY	HI	KW	P
Environ. (E)	1	39087.53 <sup>***</sup>	1487396.70 <sup>***</sup>	341475.56 <sup>***</sup>	787.95 <sup>***</sup>	121.57 <sup>***</sup>	1583.31 <sup>***</sup>
Rep/E	4	5045.24	1457792.74	169154.20	154.34	26.96	89.63
Crosses (C)	5	20935.95 <sup>***</sup>	84839.48 <sup>ns</sup>	12455.09 <sup>ns</sup>	371.68*	57.17 <sup>***</sup>	49.88 <sup>***</sup>
E x C	5	1104.45 <sup>***</sup>	86688.22 <sup>ns</sup>	26735.03 <sup>***</sup>	324.11*	8.76 <sup>ns</sup>	18.72 <sup>ns</sup>
Error (a)	20	265.91	32148.10	5629.18	92.33	3.99	8.53
Lines(L3)	114	286.76 <sup>***</sup>	33953.95 <sup>***</sup>	3751.25 <sup>***</sup>	26.82 <sup>ns</sup>	1.41 <sup>***</sup>	1.50 <sup>***</sup>
E x L3	114	143.30 <sup>***</sup>	26111.66 <sup>***</sup>	3215.87 <sup>***</sup>	32.27 <sup>ns</sup>	0.88 <sup>***</sup>	1.48 <sup>***</sup>
Error (b)	456	129.35	10644.81	1396.88	30.74	0.49	0.71

\*,\*\* significant at 0.05 and 0.01 probability levels respectively.

ns, not significant at 0.05 probability levels



Table 11. Combined analysis of variance for plant height (HT), biomass (BM), grain yield (GY), harvest index (HI), kernel weight (KW), and protein content (P) of F4 lines evaluated at Ruggs and East Farm during 1992 growing season.

Source	D.f	HT	BM	GY	HI	KW	P
Environ. (E)	1	46964.20 <sup>***</sup>	2251205.00 <sup>***</sup>	541314.67 <sup>***</sup>	1417.01 <sup>***</sup>	81.59 <sup>***</sup>	1312.20
Rep/E	4	10860.97	2063107.39	256243.14	94.96	43.07	108.53
Crosses (C)	5	21931.53 <sup>***</sup>	114156.49 <sup>***</sup>	5780.51 <sup>***</sup>	230.79 <sup>***</sup>	81.25 <sup>***</sup>	43.49 <sup>***</sup>
E x C	5	960.70 <sup>ns</sup>	9749.55 <sup>ns</sup>	7915.42 <sup>***</sup>	120.55 <sup>***</sup>	12.07 <sup>***</sup>	9.13 <sup>***</sup>
Error (a)	20	477.81	12237.82	1035.14	28.13	0.38	2.14
Lines(L4)	114	273.46 <sup>***</sup>	33716.74 <sup>***</sup>	4500.84 <sup>***</sup>	37.08 <sup>ns</sup>	1.34 <sup>***</sup>	1.99 <sup>***</sup>
E x L4	114	171.08 <sup>***</sup>	35543.39 <sup>***</sup>	4412.31 <sup>***</sup>	35.92 <sup>ns</sup>	1.05 <sup>***</sup>	1.45 <sup>***</sup>
Error (b)	456	72.33	9057.89	1180.54	32.72	0.31	0.53

\*,\*\* significant at 0.05 and 0.01 probability levels respectively.

ns, not significant at 0.05 probability level.

Table 12. Observed mean squares for plant height (HT), biomass (BM), grain yield (GY), harvest index (HI), kernel weight (KW), and protein content (P) of F3 lines evaluated at Ruggs and East Farm during 1992 growing season.

Ruggs							
Source of variation	D.f	HT	BM	GY	HI	KW	P
Replication (R)	2	3423.33	2250493.37	276359.93	92.23	52.56	173.17
Crosses (C)	5	7157.13**	82763.82	20284.81	501.11**	41.02	49.07
R*C	10	212.58	29328.84	2576.30	93.03	7.59	13.48
L3 (C)	114	138.02**	27003.3**	2779.63**	31.65 <sup>ns</sup>	1.042**	0.97**
Error	228	86.96	12421.93	1265.36	38.93	0.65	0.57
East Farm							
Replication (R)	2	6667.15	6665092.11	61948.48	216.45	1.36	6.09
Crosses (C)	5	14883.28**	88763.88	18905.31	194.67	24.91**	19.52*
R*C	10	319.24	34967.36	8682.07	91.62	0.40	3.58
L3 (C)	114	292.05**	33062.32**	4187.49**	27.44 <sup>ns</sup>	1.24**	2.02**
Error	228	171.74	8867.69	1528.39	22.56	0.33	0.85

\*\* significant at 0.01 probability level

ns not significant at 0.05 probability level

Table 13. Observed mean squares for plant height (HT), biomass (BM), grain yield (GY), harvest index (HI), kernel weight (KW), and protein content (P) of F4 lines evaluated at Ruggs and East Farm during 1992 growing season.

Ruggs							
Source of variation	D.f	HT	BM	GY	HI	KW	P
Replication (R)	2	6247.99	2706789.19	303140.58	137.41	76.05	121.56
Crosses (C)	5	7775.28**	85850.60	2561.21	103.28	33.73	27.51
R*C	10	239.32	11487.33	368.29	22.91	0.39	2.52
L4 (C)	114	166.61**	35959.69**	3036.08**	40.84 <sup>ns</sup>	0.99**	1.17**
Error	228	35.50	10253.07	1260.50	41.49	0.46	0.50
East Farm							
Replication (R)	2	15473.96	1419425.59	209345.70	52.50	10.08	95.51
Crosses (C)	5	15116.96*	38055.44	11134.72	248.06**	59.58**	25.12
R*C	10	716.29	12988.31	1701.98	33.36	0.36	1.76
L4 (C)	114	277.93**	33300.44**	5877.07**	32.16*	1.36**	2.27**
Error	228	109.16	7862.70	1100.58	23.95	0.17	0.57

\*\* significant at 0.01 probability level

ns not significant at 0.05 probability level

Table 14. Genotypic correlations between kernel weight (KW), grain yield (GY), and protein content (P) in F3 and F4 lines grown on the East Farm and Ruggs during 1992 growing season.

Cross	Location	F3 Lines			F4 Lines		
		$r_{g(kw,gy)}$	$r_{g(kw,p)}$	$r_{g(gy,p)}$	$r_{g(kw,gy)}$	$r_{g(kw,p)}$	$r_{g(gy,p)}$
Wd-Neb 021 // Cak-Mak	Ruggs	0.20	-0.88	-0.79	0.38	-0.16	-0.19
	East Farm	0.96	-0.04	-0.16	0.07	-0.51	-0.15
Wd-Neb 021 // Parus	Ruggs	0.12	-0.65	-0.36	0.13	-0.06	-0.02
	East Farm	0.02	-0.87	-0.17	0.34	-0.48	-0.89
Wd-Neb 021 // 07690 Nic	Ruggs	0.89	-0.89	-0.41	0.17	-0.32	-0.64
	East Farm	0.32	-0.72	-0.37	0.43	-0.39	-0.99
Cak-Mak // Parus	Ruggs	0.09	-0.57	-0.23	0.66	-0.07	-0.10
	East Farm	0.61	-0.98	-0.57	0.58	-0.46	-0.02
Cak-Mak // 07690 Nic	Ruggs	0.45	-0.31	-0.56	0.10	-0.14	-0.60
	East Farm	0.64	-0.02	-0.38	0.29	-0.24	-0.29
Parus // 07690 Nic	Ruggs	0.18	-0.86	-0.45	0.49	-0.34	-0.01
	East Farm	0.49	-0.28	-0.04	0.76	-0.42	-0.66

n=20

Table 15. Components of genotypic variance estimates for kernel weight (KW), grain yield (GY), and protein content (P) in F3 and F4 lines grown on the East Farm and Ruggs during 1992 growing season.

Cross	Location	F3 Lines			F4 Lines		
		KW	GY	P	KW	GY	P
Wd-Neb 021 // Cak-Mak	East Farm	0.22	738.94	0.26	0.39	565.76	0.65
	Ruggs	0.14	426.19	0.54	0.44	541.03	0.35
Wd-Neb 021 // Parus	East Farm	0.17	210.25	0.41	0.06	1520.0	0.40
	Ruggs	0.10	483.62	0.17	0.03	610.09	0.05
Wd-Neb 021 // 07690 Nic	East Farm	0.50	1987.36	0.88	0.48	2348.08	0.20
	Ruggs	0.19	309.96	0.21	0.21	565.04	0.28
Cak-Mak // Parus	East Farm	0.43	1092.25	0.36	0.43	1650.13	0.51
	Ruggs	0.21	866.57	0.13	0.12	1178.92	0.10
Cak-Mak // 07690 Nic	East Farm	0.18	538.96	0.18	0.68	1454.80	0.59
	Ruggs	0.17	604.42	0.04	0.18	302.85	0.19
Parus // 07690 Nic	East Farm	0.33	750.43	0.20	0.33	2014.22	1.06
	Ruggs	0.22	837.78	0.24	0.11	353.24	0.38

n = 20