1. INTRODUCTION

High grain yield is a prerequisite in the release of wheat genotypes intended for production under high input and capital-intensive cultures such as is practiced in Zimbabwe. Zimbabwe experiences shortages of wheat grain due to limited irrigation facilities and also due to the tropical nature of its climate, which confines wheat production to the dry, winter months, under costly irrigation regimes.

Breeding programmes serving wheat production systems which target high grain yields, such as is required in Zimbabwe should aim to generate elite wheat germplasm which carries high frequency of high yielding genotypes. Such breeding programmes should conduct efficient variety screening techniques during the promotion of advanced breeding material into replicated variety evaluation stages. This should ensure maintenance of high grain yield performance in the subsequent advanced variety testing for the purposes of variety release.

It is not feasible to evaluate a very large number of wheat lines in statistically designed experiments, under the constraints of time, resources and space. Thus only a limited number of accessions are, in time, advanced into preliminary statistically designed field experimentation with the rest being discarded. The historical dilemma facing wheat breeders has been the identification of reliable selection criteria for high grain yield performance during early breeding generations (McGinnis and Shebeski, 1968; Knott, 1972), and later in the screening of homozygous lines for advanced testing (Fischer and Kertesz, 1976; Ellison, Latter and Anttonen, 1985; Sharma, 1993). Wheat scientists have hitherto failed to identify simple plant characteristics which relate closely to grain yield potential at field crop densities. Reasons for this vary from the low additive genetic variances relative to the environmental and error variances that these simple

plant traits are associated with (Fischer and Kertesz, 1976.), to the genotype x environment interaction and the presence of allometric relationships (Grafius, Thomas and Banard, 1976). The need to establish reliable criteria to screen homozygous wheat lines prior to replicated trial testing should continue to be addressed. One solution suggested has been the use of small (micro) or hill plots for early yield testing (Frey, 1965; Jensen and Robson, 1969; Briggs and Shebeski, 1971; Ellison, *et al*., 1985). Such plots attempt to simulate to some degree, the competitive environment of a crop, given the usual limitation on seed during early testing (Fischer and Kertesz, 1976).

The utility of morpho-physiological traits; biomass, grain mass and harvest index of single row or hill plots as indicators of yielding ability has produced varying results. Fischer and Kertesz (1976) found a strong phenotypic correlation between microplot and field crop grain yield of spring wheat in Northwest Mexico. The relationships of biomass and harvest index of microplots with grain yield of large plots were not included in their investigation. Relationships of the three morpho-physiological traits; biomass, grain mass and harvest index of thinly seeded plots with grain yield in commercial stands were evaluated for hard red winter wheat in the Southern Great Plains of USA by Sharma and Smith (1987). Grain mass followed by harvest index of thinly seeded plots was strongly correlated with grain yield in field crop stands. Biomass of thinly seeded plots was only moderately correlated with grain yield of commercial stands. This investigation did not however discriminate the effectiveness of the three selection criteria over different plant structure. In a later study by Kramer, Van ooijen and Spitters (1982), moderate to strong genetic correlation between grain yield of microplots of various sizes and mean grain yields in replicated trials of spring wheat in Wageningen, The Netherlands, were obtained.

Strong associations were encountered at wide inter-row spacing than at narrow-row spacing, suggesting that the widening of inter-row spacing of micro plots may be advantageous. Again the other two selection criteria, biomass and harvest index of microplots, were not examined in their study and the influence of plant stature on the relationships of microplot grain yield and large plot grain yield, were not ascertained.

Sharma (1993) used short stature spring wheat genotypes and correlation between biomass of microplots at the F3 generation and grain yields of corresponding genotypes in replicated trials in the following year in Rampur, Nepal, under a production culture similar to that practiced in Zimbabwe. The correlated response was higher at a high productivity system. Sharma's 1993 study showed a negative relationship between biomass and harvest index. Grain mass and harvest index of microplots as selection criteria for high grain yield performance were not evaluated.

The evolution of the influence of plant stature on the relationship between biomass and harvest index of spaced plants with grain yield performance in replicated trials was attempted by McVetty and Evans (1980) in either tall or short stature groups of winter wheat cultivars. Harvest index of spaced plants was strongly correlated with grain yield among tall genotypes but biomass of spaced plants was effective among the short statured genotypes. Grain mass of spaced plants was not included as a selection criterion. More over the selection units were not in the form of microplots, but were spaced plants. It is evident that previous studies have not systematically and concurrently evaluated the effectiveness of the three morpho-physiological traits, biomass, grain mass (earmass) and harvest index (HI) of microplots, as selection criteria for high field crop grain yield performance for the purpose of establishing their relative selection efficiency. Plant

stature appears to influence the nature and degree of correlated responses of grain yield to the different auxiliary traits in question. Hence, it is important to discriminate the relative selection efficiencies of the three criteria by plant height strata.

It is expected in the study that if the confounding effects of plant stature may be removed by stratifying populations into uniform plant height strata at the advanced stages of segregation, hill plot characters such as biomass, grain mass or HI, may be more reliable in their indications of grain yield potential of wheat genotypes. Further more, if the single ear progenies are propagated in wide rows and in ideal conditions of growth, characterized by uniform soils, uniform crop establishment and uniform moisture status, it is assumed that environmental component of variation in the expression of the three single ear-to-row progeny attributes, would be minimised.

Efficient utility of auxiliary traits as selection criteria for grain yield requires information on the mode of inheritance and inter-relationships of the selection traits and the responding trait in the actual environmental conditions intended for their application. Thus inheritance and mutual association studies on grain yield and the auxiliary traits used in this study should be conducted under the wheat production conditions of Zimbabwe.

The hypotheses tested in this study were:

1. The effectiveness of indirect selection for grain yield of wheat (*Triticum aestivum* L.) using auxiliary triats; biomass, earmass and harvest index of single-ear progeny plots is similar in the three selection criteria and is not influenced by height of the plant.

2. The mode of inheritance of grain yield of spring wheat and those of its related traits; biomass, earmass, HI, number of productive tillers and plant height under the irrigated and heavily fertilized culture in Zimbabwe, are predominantly additive in expression and are environmentally stable.

The above hypotheses were tested by the following objectives:

1. To measure the direct selection response of grain yield of spring wheat genotypes in replicated trials at two locations.

2. To measure and discriminate the relative selection efficiencies of single-ear progeny traits; biomass, earmass and HI in the indirect selection for grain yield of wheat over different plant height strata.

3. To ascertain correlated responses to selection among the selection traits by measuring phenotypic and genotypic correlations among them.

4. To study the inheritance of grain yield and the related traits; biomass, earmass, HI, number of productive tillers and plant height, under Zimbabwean irrigated conditions over two locations.

2. LITERATURE REVIEW

2.1 Selection criteria

Indirect selection for grain yield of wheat using yield component traits has been widely investigated yielding inconsistant results. The use of grain yield of single plants or of wheat microplots as indicators of yield performance in commercial planting has given inconsistent results because grain yield is a complex character which is subject to high genotype x environment interaction (Latter and Ellison, 1984). In some instances reported by Whan, Rathjen and Knight (1981) and by Sharma and Smith (1987), grain yield of microplots was however a better predictor of crop performance than biomass and Harvest index. Harvest index (HI) was described by Donald (1962) as the ratio of grain yield to total above ground biomass yield. Donald (1962) also stated that HI is an important aspect of differential partitioning of photosynthate and that, improved HI represents an increased physiological capacity of the crop to mobilise photosynthate and translocate it to organs of economic value. Harvest index is thus a useful measure of sink capacity of a cultivar. Donald and Hamblin (1976), Takeda and Frey (1985) and later Hay and Walker (1989), expressed the grain yield as the product of biomass and HI. Sharma and Smith (1986) contended that grain yield of cereals can be improved by increasing biomass without changing HI or by improving HI keeping biomass constant, or by increasing both biomass and HI.

2.1.1 Association between auxiliary traits and field crop grain yield including their heritabilities

The prerequisites to successful indirect selection of a character via a secondary trait are firstly, high genetic correlation between itself and the secondary trait and high heritability values in the secondary trait relative to the responding trait (Lerner, 1958; Falconer, 1981). Fischer and Kertesz (1976) estimated phenotypic correlation between grain yield of spaced plants and large plot grain yield and also that between grain yield of microplots and grain yield of large plots, using means of 34 spring wheat genotypes in North West Mexico. They found a weak but statistically significant phenotypic correlation between grain yield of spaced plants and large plot grain yield. That between microplot grain yield and grain yield was stronger and highly significant ($r_p = 0.67$). A strong phenotypic correlation (0.72) between grain yield of very thinly seeded plots and grain yield at standard spacing was also obtained by Sharma and Smith (1987) in an experiment with winter wheat in Oklahoma, U.S.A. Kramer, *et al*. (1982) reported moderate to strong genetic correlations between grain yield of microplots of various sizes and grain yield in trials of spring wheat in Wageningen, The Netherlands. Single-row plots spaced 20cm apart gave a genetic correlation of 0.64 while, singe-row plots spaced 40cm apart gave a genetic correlation of 0.83. The larger single plots and their respective centre rows, discarding single border rows, gave even higher genetic correlations, being 0.98 and 1.08 for the 3-row and 6-row plots, respectively, and 1.66 and 1.18 for the respective centre rows of the 3-row and 6-row plots.

The relationships between grain yield of wheat and biomass yield of either hill plot or field crops has been reported in relatively few investigations when compared to that of HI and grain yield. Grain yield is however a constituent of biomass, hence explicit functional relationships are expected between biomass and grain yield. The problem in working with biomass is its proneness

to high environmental variability (Donald and Hamblin, 1976). In the North Mexican Spring Wheat experiment of Fischer and Kertesz (1976), biomass of spaced plants was not at all related to grain yield of wheat in large plots. The opposite was reported by McVetty and Evans (1980) who studied seven tall and seven semi-dwarf spring wheat genotypes in spaced plantings. They found a significant phenotypic correlation between biological yield of spaced plants and grain yield at commercial crop stands in the tall statured genotypes only. There was however no relationship between these attributes in the short statured genotypes. In the study of Sharma and Smith (1987) with winter wheat, biomass yield in low stands correlated well with grain yield in low stands but correlated only moderately with grain yield in standard spacing ($r_p=0.43$; $P<0.05$). In the same experiment phenotypic correlation between biomass yield in standard spacing and grain yield, also in standard spacing, was moderate to high.

Biomass apparently relates very closely to grain yield for spring wheat grown under rainfall conditions. For instance a high positive phenotypic correlation between biological yield and grain yield was obtained for 10 spring wheat genotypes grown in trials at nine locations in Ethiopia (Geleta, Gebre - Mariam, Tesemma, Gebeyehu and Van Ginkel, 1991). In the same study, HI was only weakly correlated with grain yield of rainfed spring wheat ($r_p = 0.25$).

It is upon the recent results from studies on biomass yield of spring wheat by Sharma (1993) in an environment similar to that in Zimbabwe that confidence in using biomass as a selection criteria for high grain yield may be derived. Sharma (1993) obtained high positive genotypic correlations between biomass yield and grain yield (values ranging from 0.69 to 0.91) across the eight spring wheat populations grown in Nepal.

Harvest index has been found to be positively correlated with grain yield in several studies with phenotypic correlation coefficients ranging from 0.62 to 0.96 (Syme 1970; Singh and Stoskopf, 1971; Nass, 1980). Syme (1972) found a phenotypic correlation of 0.85 between HI and mean plot grain yield measured in single plants grown under greenhouse conditions over 63 international sites. Fischer and Kertesz (1976) grew a set of 40 homozygous genotypes as spaced plants and in large plots at Obregon in Mexico under uniform conditions of irrigation and fertility. Phenotypic correlations of 0.56 and 0.66 with plot yield were recorded for whole plant and main branch or shoot harvest indices measured in spaced plants. Batt and Derera (1978) reported a genetic correlation of 0.89 between harvest index in 20-grain hill plots spaced 50 cm apart and large plot yield at the same site in the following year. In a study on winter wheat in Oklahoma, USA, Sharma and Smith (1986) recorded moderate to high phenotypic correlation values (0.57 to 0.78) between HI and grain yield of three F3 populations and relatively low phenotypic correlations values between the two attributes (0.29 to 0.38) in the following year in the F4 generation of the three winter wheat populations. Reasons for the reported differences in the phenotypic relationship between the two attributes may be indicative of a preponderance of environmental correlations and/or low genetic correlation between them.

Sharma and Smith (1987) also obtained a moderate phenotypic correlation ($r_p = 0.60$) between harvest index and grain yield of winter wheat at standard spacing and a slightly higher correlation between harvest index at low plant densities and grain yield at standard spacing ($r_p = 0.67$), but the association between harvest index and grain yield at low seeding rates was exceptionally low ($r_p = 0.34$). Sharma, Smith and McNew (1987) noted that HI was significantly correlated ($P<0.01$)

with grain yield of winter wheat ($r_p = 0.62$) in low yielding environments but not in highly productive environments ($r_p = -0.17$). McVetty and Evans (1980) found strong phenotypic

correlation (rp = 0.76) between harvest index of seven spaced-planted semi-dwarf spring wheat genotypes and their grain yield in commercial planting.They however obtained poor and non significant correlation (rp = 0.06) between the same attributes in seven tall statured spring wheat genotypes in Canada.

Heritability estimates for biomass yield in cereals have been reported to be low to high (Helsel, 1985), depending on the accuracy in measuring this character and also on the degree of uniformity of the environments sampled. Biomass yield is inherently variable among individuals and is highly sensitive to environmental changes. It is however encouraging to note that in the recent study of Sharma (1993), on the selection for biomass yield in spring wheat, moderate to high realized heritability estimates (0.49 to 0.85) were obtained in the high fertility production system which is similar to that practiced in Zimbabwe. Londero, Biasutti and Maich (2000) also obtained realized heritabilities which were intermediate (0.31) for biological yield in spring wheat in Argentina, but low (0.15) for HI.

In their synopsis on the inheritance of single plant characters in wheat, Paroda and Joshi (1970) noted that grain yield gave low narrow sense heritabilities due to large non-additive genetic and environmental variances. This was later corroborated by the results of Ketata, Edwards and Smith (1976) who obtained a narrow sense heritability of 0.16 for grain yield per plant in a winter wheat cross. Entry mean heritabilities for grain yield have been found to be low to moderate depending on cultural conditions of growth. Kramer, *et al*.(1982) obtained an entry-mean heritability estimate of 0.64 in a trial with sixteen spring wheat varieties and four replicates. In the same experiment, the range of heritability estimates for grain yield of plots of various sizes was 0.07 to 0.46. A very large entry mean heritability estimate (0.84) for grain yield was reported by

Amin, Barma and Razzaque (1992) in durum wheat in Bangladesh. These authors also reported high entry mean heritability estimates for HI (0.80) and for biological yield (0.70).

Harvest index of cereals is generally associated with moderate to high heritability estimates. Moreover HI, being a ratio, is expected to be less subject to variation than other variables. Rosielle and Frey (1975) reported intermediate values of broad sense heritabilities (0.35 to 0.66) for harvest index in oat lines derived from a bulk population. Those reported by Batt (1976) in eight spring wheat crosses were intermediate to high in magnitude (0.48 to 0.88). Realized heritability estimates calculated as the ratio of the differences of high and low HI groups in two consecutive generations of inbreeding were found to be high (0.70 and 0.88) in the study by Batt (1977) using F2 and F3 generations of two spring wheat crosses in Australia. They were found to be moderate in magnitude (0.44 to 0.60) in the study of Sharma and Smith (1986) using F3 and F4 generations of winter wheat in Oklahoma, USA. Gene action governing the expression of HI has been found to be largely additive (Batt, 1976) in the regression of F2 generation on F3 generation of two spring wheat crosses.

2.1.2 Association between auxiliary traits

It is important in this study to review previous findings on the associations between the auxiliary traits in so far as this information bears relevance to the correlated response of the responding trait, grain yield.

Detection of strong genetic correlations among the auxiliary traits may present the opportunity of using that auxiliary trait which is easiest to measure and is least subject to sampling variation even if the other auxiliary traits bear slightly stronger genetic relationships with the responding trait, grain yield. Presence of genetic correlations between plant stature and the auxiliary traits

would suggest the need for plant height stratification in their application as secondary traits in the selection for grain performance, with the corollary being true. The associations between plant height and traits of interest will be reviewed first. Correlation between plant height and grain yield of single plants or grain yield of hill plots have been found to be positive in most studies. The study by Johnson, Biever, Haunold and Schmidt (1966) on a hard red winter wheat cross showed a moderate positive and significant phenotypic correlation (0,37; $P<0.01$) between plant height and grain yield of single plants. The genotypic correlation between these attributes although positive, was low ($rg = 0.13$) and nonsignificant. Sharma and Smith (1986) found weak phenotypic correlations between plant height and grain yield of F3 and F4 winter wheat plants in Oklahoma (USA), which tended to be negative ($rp = 0.01$ to -0.28).

In another winter wheat study, Sharma, Smith and McNew (1987) found a significant positive phenotypic correlation (0,64; $P<0.01$) between plant height and grain yield over twelve environments in Oklahoma. This relationship reduced to a very weak one when the environments were stratified into high productivity sites ($rp = 0.17$) and low productivity sites ($rp = 0.15$). In standard plant densities of wheat, plant height has been found to be negatively correlated with grain yield and harvest index. Jenings (1964) noted that the yield improvement in cereals has been achieved by breeding plant types which are short statured with high harvest indices. The short stature also confers resistance to lodging, thus allowing cultivars to benefit from higher fertilizer rates. In Australia, Fischer and Quail (1990) studied the effects of major dwarfing genes on yield potential in spring wheats. In their experiment, the Rht1 + Rht2 dwarf genotypes gave the highest yields while the Rht3 , Rht2 and the Rht1, on average yielded 3 percent, 9 percent and 11 percent lower than the double dwarf genotypes. The non dwarf or tall group yielded 24 per cent lower than the double dwarf genotypes. These yield differences were positively associated

with HI. A negative association between plant height and grain yield of wheat at Standard spacing (500 seeds /m^2) was also found by Collaku (1994) in winter wheat in Albania.

The phenotypic correlation between the two attributes in the 169 F2 derived lines in F5 at three lowland sites was (-0.16; P< 0.05) and the genotypic correlation was (–0.44; P<0.01).

Negative association between harvest index and plant stature in wheat is implicit in the study of Allan (1983) who found the two and one- gene semi-dwarf doses to increase harvest index of spring wheat by 31 and 20 per cent respectively. The overall mean HI of two-gene semi-dwarf (short), one-gene semi-dwarf (medium) and normal (tall) were 41.8, 38.0 and 31.6 per cent respectively. In winter wheat, Sharma and Smith (1986) obtained highly significant negative phenotypic correlations between single plant harvest indices and grain yield in Oklahoma (USA). The range of these phenotypic correlations over three populations in the F3 was -0,46 to –0.56 (P<0-.01) and that in the corresponding F4 populations was – 0.73 to 0.91 (P<0.01). These results were further corroborated by those obtained in the following year by Sharma *et al.* (1987) in winter wheat grown in trials over twelve environments, also in Oklahoma (USA). In this latter study a negative phenotypic correlation of –0.43 (P<0.01) was obtained between plant height and harvest index over the total of 12 sites and a similar correlation (rp= -0.40; P<0.01) was obtained for the six sites situated in the low grain yield potential areas . The negative association between these two attributes in the six high productivity sites was even stronger
(rp = -0.80; P<0,01).

In wheat, tall plants with high harvest index would be expected to possess higher biomass than short plants with high harvest index. Harvest index however tends to be negatively associated with plant stature. Thus the relationship between biomass and plant height in wheat appears to be

dependent on the genetic background of the material. The study of Sharma and Smith (1987) on winter wheat in Oklahoma (USA) showed positive and moderate phenotypic correlations (0.50 and 0.40 ($P<0.01$) respectively between the F3 and F4 generations of one of the three populations which were tested. Biomass yield was also positively correlated (0.34; $P<0.05$) in the F3 generation only but not in F4 generation ($rp= 0.13$) of one of the populations. The third population gave very weak associations between the two traits ($rp = 0.04$ and 0.31) in both the F3 and the F4 generations.

The relationship between harvest index and biological yield has tended to be negative ranging from weak to medium in strength. In winter wheat the phenotypic correlation between biomass yield and HI of single plants in F3 and F4 generations of three populations in the study of Sharma and Smith (1986) ranged between 0.06 and –0.34 ($P<0.05$). The phenotypic correlation coefficient was also negative (-0,31) but not statistically significant in durum wheat in replicated trials conducted by Amin, Barma and Razzaque (1992) in Bangladesh. A more elaborate study of the relationship between biomass yield and harvest index was conducted by Sharma (1993) on irrigated spring wheat in Nepal under similar conditions to those in Zimbabwe. Sharma (1993) obtained significant negative simple correlations (-0.36; $P<0.05$ to –0.60; $P<0.01$) between the two traits in four out of the eight populations grown in high fertility regimes. The remaining four populations gave weak nonsignificant simple correlations in the same production environment ($rp = 0.11$ to –0.21). The simple correlations between biomass yield and harvest index were generally low and nonsignificant in the low fertility regimes for all the eight populations ($rp = 0.00$ to –0.24). The genotypic correlations (0.08 to –0.51) between biomass yield and HI in the study of Sharma (1993) for the eight populations in the F4 generation were low to moderate and predominantly negative.

Sharma and Smith (1986) found significant (P< 0.01), moderate to high phenotypic correlations (0.66; P<0.01 to 0.70; P< 0.01) between biomass yield and grain yield of single plants measured in the F3 generation of three winter wheat populations in Oklahoma (USA). The phenotypic correlations (0.80 to 0.91) were even stronger and significant (P< 0.01) in the corresponding F4 generation of the three populations. In the following year, Sharma and Smith (1987) reported another strong simple correlation between biomass yield and grain yield (0.87; P< 0.01) for winter wheat grown at low seeding rates in Oklahoma in 1984 and 1985. In their study the simple correlation (0,68; P< 0.01) between the two traits was moderate to strong when measured at standard spacing. Amin *et al.* (1992) however found a non-significant phenotypic correlation (0,21) between grain yield per plot and biomass per plot in a three-replicate trial conducted on durum wheat in Bangladesh. The strongest simple correlations (0,82 to 0,96; P< 0.01) between biomass yield and grain yield were obtained by Sharma (1993) in irrigated spring wheat grown in both high and low fertility regimes in Nepal. Genotypic correlations between biomass yield and grain yield in the F4 generation of the eight spring wheat populations were also high and positive (0.69 to 0.91).

2.1.3. Stability across environments

The presence of genotype x environment interaction reduces the correlation between phenotype and genotype and thus hampers selection progress. Sharma *et al.* (1978) measured the stability of HI and grain yield in winter wheat at six sites in Oklahoma (USA) over a period of two years. Apart from high genotypic differences for HI and grain yield, they found significant genotype x year x location interactions for both traits. It is worth noting that in their study, both the genotype x year and the genotype x location interactions were not significant. Hence selection conducted over different locations in the same year, would have been effective. In Australia, Ellison, Latter

and Anttonen (1984) also noted genotype x site x year interaction as the major component of the genotype x environment interaction in both harvest index and grain yield.

In their study genotype x year interaction component was not significant in periods 1968 - 70 and 1972 - 73, but was of major importance in 1977 - 78.

Stability of auxiliary traits across different cultural conditions would increase their effectiveness in indirect selection for the responding traits of interest. For instance HI has been found by several cereal scientists to be stable across different seeding rates. In Australia, Batt and Derera (1978) found no evidence of genotypic interaction for harvest index of wheat measured in hill plots in 1975 and that measured in large plots in 1976. In a later study of the effects of seeding rates on harvest index, grain yield and biomass yield in winter wheat in Oklahoma (USA), Sharma and Smith (1987) found high simple (0.92) and rank (0.95) correlation coefficients for HI of different crop densities. High simple (0.86) and rank (0.90) correlation coefficients were also found for biomass between the low and high seeding rates. They however obtained low to moderate simple (rp=0.72) and rank (rp=0.50) correlation coefficients between grain yield at low seeding rates and grain yield at standard seeding rates. The results of Baker (1982) in a similar, but earlier study with eight spring wheat cultivars in Canada, showed a similar trend to those of Sharma and Smith (1987) in low productivity regimes only. Baker (1982) however reported marked effects of seeding rates on genotypic ranks of both HI and biomass.

2.2 Genetic parameters

An understanding of the genetic parameters that influence selection progress is essential in the choice of appropriate selection techniques in the genetic improvement of characters. In particular the amount and type of genetic variation in the base population under selection prescribes the

breeding strategy and determines the gains which can be obtained from selection (Hallauer and Miranda, 1981).

2.2.1 Hereditary Variance and its estimation

The value observed when a metric character is measured is the phenotypic value whose expression is a sum of genetic, environmental and sometimes the genetic x environmental interaction effects (Falconer, 1960). Hallauer and Miranda (1981) defined the linear model describing the phenotype of an individual, i, as

$$Pi = u + gi + ei + (ge)i$$

Where,

Pi = phenotype, sum of all model components,

u = overall mean,

gi = genotypic effect,

ei = environmental effect, and

(ge)i = genotype x environmental interaction effect.

Cockerham (1956a) described the genotypic effect for a particular genotype as the difference between the mean of all the phenotypes with that genotype and the mean of all the phenotypes in the population. Hence the genotypic effect is defined only in contrast with other genotypes in the same environments. The changes in relative contrasts among genotypes or more specifically the changes in order, ranking and relative values among genotypes is then defined as the genotype x environment interaction. Since selection operates on available variation within a population, the importance of a study of variation of a character centres on the ability to partition its variation into components attributable to different causes (Falconer, 1960).

If genotypes and environments are not correlated in their effects, the total phenotypic variance is constituted by the genotypic, environmental and genotype x environment interaction variance (Cockeham, 1954) so that

$$Vp = Vg + Ve + Vge$$

Where Vp = phenotypic variance,

Vg = Genotypic variance,

Ve = phenotypic variation caused by variation in the environment , and

Vge = variation due to interaction between genotype and environment.

Proper experimental designs in which genotypes are randomly distributed relative to environmental variation within single environments and repeated over environments will minimise genotypic and environmental correlation and permit estimation of the three principal components of the phenotypic variance (Searle, 1971).

The genotypic variance (Vg) can be subdivided into different components. Fisher (1918) demonstrated that the hereditary variance in a random mating population can be partitioned into three parts:

(i) an additive portion associated with average effects of genes (Va),

(ii) a dominance portion due to allelic interactions (Vd), and

(iii) a portion due to non allelic interactions or epistasis (Vi)

The epistatic variance component was further defined by Cockerham (1954) and Kempthorne (1954) according to the fractional interaction of the various genetic effects thus:

(i) Vaa, Vaaa, etc epistatic variance due to interaction of additive effects of two, three or more loci

(ii)Vdd, Vddd epistatic variance due to interaction of dominance effects of two, three or more loci, and

(iii)Vad, Vaad, Vadd, epistatic variance due to interaction of additive and dominance effects involving two, three or more loci.

The total genotypic variance is only of hereditary significance in mass selection where individual genotypes are selected solely on the basis of their phenotypic expression. In this case, the selection unit is also the recombinant unit in terms of the entire genotypic constitution (Hallauer and Miranda, 1981). This procedure is usually applied in the final selection of superior lines out of heterogeneous populations of homozygotes. In the breeding procedures where parental genotypes are selected and mated to generate new recombinant types or offspring, the ability of the parents to transmit superior genes to their offspring becomes important. Since parents pass on their genes and not their genotypes (Falconer, 1981), it is the average effect (over all loci and alleles) of those genes transmitted to the offspring that constitutes the breeding value of the parents.

The variance of the breeding values is termed the additive genetic variance (Va). It is therefore the additive genetic variance which is the major cause of resemblance between parents and offspring (Robinson, Comstock and Harvey, 1949).

The presence of large additive genetic variance shows that selection, either of single plants or among progenies, should be effective in improving the character in segregating populations (Robinson, Comstock and Harvey, 1955). It is the additive and the additive x additive genetic

variance components that are fixable and have the property of hereditary predictability (Mashiringwani, 1993 after Jain and Singh, 1978). This is the nature of genetic variation which is expected among a mixture of homozygous lines of wheat The presence of dominance genetic variation indicates that improvements that lead to development of homozygosity are not appropriate. The methods that are suitable are those that allow detection and selection of the superior heterozygous genotypes (Sprague and Tatum, 1942). Epistatic variance is the deviation from the additive - dominance linear model. Its presence biases the dominance variance estimate upwards thereby reducing the additive genetic variance component (Robinson, Comstock and Harvey, 1955). Thus in a self pollinating species such as wheat, dominance genetic variation and epistatic genetic variation prevents detection of superior performing genotypes before fixation at complete homosygosis (Snape, 1987).

The expressions given by Mather (1949) and Mather and Jinks (1971) for genetic variance components expected in the successive generations of a cross between inbred lines are described for the different generations. For instance, the total genetic variance of the F2 population can be estimated by using parental and F1 generations of the parents, the F1 population (the non - segregating generations) to provide an estimate of the environmental effects, according to Mather and Jinks (1971) i.e;

$$VF2 = Va/2 + Vd/4 + E2$$

Where,

VF2 = variance of F2 population,

Va = additive genetic variance,

Vd = dominance genetic variance, and

E2 = error variance among individual plants

Backcross generations can also be made by crossing the F1 generation with the respective parents to generate the first backcross generation (BC1 and BC2); for parents one and two respectively. Expressions for the different generations can be used to estimate additive and dominance variances since one can combine the equations where the effects are of similar magnitude (Hallauer and Miranda, 1981). As an example, additive genetic variance can be estimated from the difference of the sum of variance of two first backcross generations and twice the variance of F2 (Warner, 1952) i.e.

$$2VF2 - (VBC1 + VBC2) = Va/2$$

2.2.2 Definition and estimation of Heritability

The foregoing partitioning of variance into its different components enables the estimation of the relative importance of the determinants of the phenotype, in particular the role of heredity versus environment or nature and nurture (Falconer, 1981). The ratio of the total genotypic variance (Vg) to the total phenotypic variance (Vp) i.e. Vg/VP, expresses the extent to which individual phenotypes are determined by their genotypes. It is termed the heritability in the broad sense (h^2_{bs}) or the degree of genetic determination (Allard, 1960; Falconer, 1981), and is only relevant in mass selection where individuals are selected out of a population of homozygous genotypes on the basis of their phenotypic expression. In this case, selection operates on the total genotypic variance since the selected genotype is the recombinant genotype (Hallauer and Miranda, 1981).

It is only the additive genetic component of variation (Va) that has the quality of predictability that is needed in designing breeding strategies (Stansfield, 1983). The ratio of the additive genetic variance (Va) to the total phenotypic variance (Vp) i.e. Va/Vp, expresses the extent to

which offspring phenotypes are determined by the genes transmitted from the parents or by the breeding values of the parents.

This is called the heritability in the narrow sense (h^2) (Allard, 1960; Falconer, 1981). The two heritabilities can be expressed in terms of the `genetic components of variance (Simmonds, 1979) as follows:

(i) Heritability (broad-sense) becomes

$$\frac{Vg}{Vp} = \frac{Va + Vd}{Va + Vd + Ve}, \text{ and}$$

(ii) Heritability (narrow sense) is

$$\frac{Va}{Vp} = \frac{Va}{Va + Vd + Ve}$$

Where,

Vd = dominance genetic varance, and

Ve = error variance ,

with remaining terms described as above.

The presence of epistatic gene effects (which are assumed absent in the estimation of additive and dominance genetic effects) operates to reduce the estimates of additive genetic variances causing a proportionate increase of estimates of the dominance genetic variance (Mather, 1949), thereby causing a downward bias in the estimation of the narrow sense heritability (Hallauer and Miranda, 1981).

Allard (1960) used the variances of the six generations of crosses between two homozygous genotypes in the estimation of broad and narrow sense heritabilities. Variances of the two parental generations (VP1 and VP2), those of the F1 and F2 generations (VF1 and VF2) and those of the two first backcross generations (VBC1 and VBC2) were organised to generate the broad sense heritability as follows:

$H^2 = [VF2 - (VP1 + VP2 + VF1)/3]/VF2$

and the narrow sense heritability as

$h^2 = [2VF2 - (VBC1 + VBC2)]/VF2.$

The model of Campbell and Lafever (1978) for narrow sense heritability estimation differs from the above in that the estimation of the error variance is taken as the square root of the product of the variances of the parental generations i.e.

$h^2 = [VF2 - (VP1:VP2)^{1/2}]/VF2.$

The derivation of the two heritability formulae is based on the expectation of the genetic components of variance in the different generations (Mather and Jinks, 1971):

$VF2 = Va + Vd + Ve,$

$VBC1 + VBC2 = Va + 2Vd + 2Ve,$ and the

Error term (Ve) is estimated from the variance of the non segregating generations as

$Ve = (VP1 + VP2 + VF1)/3.$

Heritability ratios can also be estimated from phenotypic variance components in experiments in which a group of genotypes is grown in a series of random environments. Combined analyses over the sampled environments were described by Le Clerg, Leonard and Clark (1962). The appropriate choice of the model in the estimation of the variance ratio as estimators of the heritabilities were discussed by Comstock and Moll (1963). The estimates of variance components are obtained in the usual way from linear functions of mean squares, using estimated mean squares in lieu of the expectations (Comstock and Robinson 1952; Comstock and Moll, 1963). In the estimation of the variances, the experiments are assumed to be a balanced set and all the effects are considered random, normal, independent deviates with expectations equal to zero, and generating variances of corresponding designations (Gordon, Byth and Balaam, 1972). An example of this type of analysis is provided by experiment with Korean Lespedeza reported by Hanson, Robinson and Comstock (1956). In this experiment, several families descendant from three crosses were tested at F4 generation stage over two replications at each of two locations in each of two years. The two locations differed in soil type.

Thus the total variance (Vp) among the means of G families compared in R replications, L locations, and Y years is given by:

$$Vp = \frac{Vg}{L} + \frac{Vgl}{Y} + \frac{Vgy}{LY} + \frac{Vgly}{RLY} + Ve$$

Where, Vp = total phenotypic variance

Vg = a genetic component arising from genetic differences among families,

Vgl = a variance component arising from interaction of families and locations,

Vgy = the family by year interaction component of variance,

Vgly = the family by location by year interaction component of variance, and

Ve = the error variance.

The estimates of the genotypic variance (Vg) can vary greatly depending on the environmental unit for which the variances are considered (Allard, 1960).

The precision with which Vg is estimated increases as more and more genotype by environment interaction variances are disentangled from the genotypic variance. Dudley and Moll (1969) recommended that experiments designed to estimate variance components to be used in heritability estimates must be grown in an adequate sample of environments from the environmental population to which predictions will apply so that;

(i) the estimate of genetic variance will be free of genotype by environment interaction variance, and

(ii) the appropriate fractions of the various genotype by environment interaction components can be included in the estimate of phenotypic variance.

In situations where genotypic interactions with either locations or years are significant but are not evaluated, Allard (1960) and Dudley and Moll (1969) showed the respective extent of biases in the estimation of variances that constitute the heritability ratios. If only one location in one year is used the estimate of genetic variance includes Vgl, Vgy and Vgly in addition to Vg thus biasing the numerator of the heritability estimate upwards by Vgl + Vgy + Vgly. When genotypes are compared over more than one year in one location the genetic variance estimate is biased upwards by Vgl and the genotype by year interaction variance estimate is also biased upwards by Vgly. Similar biases occur when comparisons are made at two or more locations in one year, the estimable variances then being;

(Vg + Vgy) and (Vgl + Vgly) for the genotypic variance and the genotype by location interaction variance, respectively.

It is important to note that the genetic variance to be included in the numerator of a heritability estimate depends on the type of selection to be practised and the kind of variety to be used (Hanson, 1963). In the evaluation of homogenous varieties like clones, F1 hybrids or homozygous genotypes (inbred lines), selection is based on the total genotypic variance. However Vg among homozygous lines includes only additive genetic variance (Va) and additive x additive types of epistatic variance. Thus in the absence of epistasis, the genotypic line component of variance estimates the Va and its ratio over the phenotypic variance, would estimate narrow sense heritability (Dudley and Moll, 1969). In the case of F1 hybrids and clones the genotypic variance Vg includes all types of genetic variance, hence only heritability in the broad sense can be estimated. Heritability estimates are of major importance in biometrical genetic research. Knowledge of how precisely they have been estimated is equally important. The sampling variance of heritability ratios estimated from phenotypic variance components has been treated by Gordon, Byth and Balaam (1972). For most practical purposes however the approximate standard error (SE) of such a heritability ratio is calculated according to the estimation of Dickerson (1969) as:

$$SE(h^2) = \frac{SE(Vg)}{Vp}, \text{ in which}$$

The variance if the genotypic variance V(Vg) is estimated using Comstock and Moll (1963) formula so that:

$$V(Vg) = \frac{1}{n^2} \sum_{n} \frac{2[E(MS_u)]^2}{f_u}$$

where n = the divisor appropriate in the estimator of Vg,

$E(MS_u)$ = the u^{th} mean square in the estimator of Vg, and

f_u = the degrees of freedom of the u^{th} mean square.

The approximation of SE(h^2) assumes a symmetrical distribution in h^2 which in most cases, is not met. The measure of precision which does not rely on the underlying distribution of h^2 is the exact confidence interval method of Knapp, Stroup and Ross (1985). Examples of such confidence intervals have been derived for h^2 on a progeny mean basis and also applied to half-sib family data (Knapp *et al.,*1985). The exact confidence for heritability is expressed as

$P\{1-[M1/M2)\ F1-\alpha/2:df2,df1] \leq 1-(\sigma 2/\sigma 1) \leq 1-[M1/M2)\ F\alpha/2:df2,df1] -1\} = 1-\alpha$ where

P = percent probability,

M1 = genotypic mean square,

M2 = genotypic x environment mean square,

F(df2,df1) = value of the f distribution for degrees of freedom appropriate in the estimation of M1 and M2 respectively.

$1-\sigma_2/\sigma_1$ = Heritability, and

α = level of probability.

Gilbert (1973) commented that the estimation of genetic variance and its components have the statistical weakness of being unrobust. Slight departures from normality affect the precision of their estimation. Furthermore, they may also be inaccurately estimated because the variance of a variance contains a squared term so, the larger they are the less accurately they are known.

Fisher(1918) and Lush (1948) proposed the use of parent - offspring or mid parent - offspring regressions to estimate heritability. Since the regression of offspring on parents measures the degree of resemblance between offspring and their parents, these techniques therefore yield estimates of narrow sense heritability that are amenable to precise estimation (Simmonds, 1979).

The two commonly used regression estimators are (I) $h^2 = 2b$ (Fisher, 1918) and

(ii) $h^2 = b$ (Lush, 1948).

The first of these is an appropriate estimator in a bisexual population when the parent is non-inbred as in a random-mating population. Similarly, the second estimator is appropriate in a self - pollinated population if the parent is non - inbred, as for example, the regression of F2 on its single cross F1 parent. If the parents are inbred or related, Smith and Kinman (1965) have shown that the previous inbreeding will cause an upward bias in the estimate of heritability. Smith and Kinman (1965) then gave the correct estimator for the general case as b/(2rxy), where rxy is a measure of the relationship between the parent Y and its offspring X (Kempthorne, 1957). Smith and Kinman (1965) also presented a table of coefficients of parentage and heritability estimators for various parent-offspring relationships under continuous self - pollination.

Response to selection (R) can be used as a means of estimating heritability (h^2) in the base population if the selection differential (S) is known. Response is equal to the product of the heritability and the selection differential (Falconer, 1981) i.e.

$$h^2 = \frac{R}{S}$$

Such an estimate is termed Realized heritability. The estimation of realised heritabilities and the sampling variances of those estimators have been described by Hill (1972) for selection experiments in one direction and also for divergent selection.

The foregoing description of estimating heritability shows that this parameter (h^2) is specific to the material under study and to the structure of the experiment (Hanson, 1963; Simmonds,1979). The numerator of h^2 is partly a function of the parental difference; since parents that differ little in respect to a character cannot generate large Va or Vg in their progeny. The numerator of h^2 is also a function of the experimental design in separating Va from Vg. In the estimation of h^2_{bs}, the size of the numerator (Vg) and the denominator (Vp) are both determined by genetic differences (Vg) and by the environmental variance (Ve). Obviously Ve can be reduced by experimental

design that reduces the estimate of Ve, e.g. large plots, more replications etc. Offspring - parent regressions similarly depend upon the magnitude of genetic differences between parents and control of error. Bigger plots, larger families more replications and repeated measurements on individuals will tend to increase the numerator (covariance) of the regression coefficient and reduce the denominator (parental variance) resulting in an increase in the estimate of the heritability coefficient.

The most important function of the genetic parameter h^2 is its predictive role, expressing the reliability of the phenotypic value as a guide to the breeding value (Lerner 1958). By regarding the heritability as the regression of genotypic value (for broad sense h^2) or breeding value (for narrow sense h^2) on the phenotypic value, the genotypic value or the breeding value is then the product of phenotypic value and the broad sense or narrow sense heritability, respectively (Baker, 1986 ; Falconer, 1981). The prediction formula for genotypic value becomes (Baker,1986):

Gi	=	P + bgp (Pi -P); where
Gi	=	estimated genotypic value of an individual,
Pi	=	measured phenotypic value with genotypic value (Gi)
P	=	phenotypic mean of all individuals, over the reference set of environments, and
bgp	=	h^2 , i.e. regression of genotypic value on phenotypic value,
	=	(Vp - V)/ Vp

Similarly the prediction formula for estimating breeding value is (Falconer, 1981);

A	=	h^2p; Where
A	=	breeding value

h^2 = ratio of additive variance,Va, to phenotypic variance,Vp

= b_{AP}, i.e regressions of breeding value on phenotype,

= narrow sense heritability, and

p = phenotypic value.

Thus, if the heritability values and the phenotypic values are known, the corresponding genotypic values or additive genetic (breeding) values can be estimated.

2.2.3 Correlation of characters

The determination of nature and degree of association between characters is necessary in the identification of efficient selection traits. This study involves the indirect selection of high yielding wheat genotypes using hill plot traits that are positively correlated with grain yield of commercial stands. However, both the heritability of the selection trait and the correlation between itself and the responding trait are important in determining whether indirect selection is more efficient than direct selection. The association between characters that can be directly observed is the correlation of phenotypic values or the phenotypic correlation. This is usually termed the simple or Pearson's product moment correlation, and is defined as the ratio of total phenotypic covariance between traits to the product of their phenotypic standard deviations (Falconer, 1981) i.e.

$$rp = \frac{\text{cov } P_{xy}}{(VP_x \bullet VP_y)^{1/2}}$$

where, rp = phenotypic correlation,

$\text{cov } P_{xy}$ = phenotypic covariance of x and y,

VP_x = phenotypic variance of x, and

VP_y = phenotypic variance of y.

Lerner (1958) defines the phenotypic correlation as a compound of environmental and genetic correlations. In genetic studies, it is necessary to distinguish between the two causes of correlation. Environmental correlations, which are strictly speaking, the correlation of environmental deviations (Falconer, 1981), may be removed from the total phenotypic correlation to remain with the genotypic correlation. In principle, there are also correlations between dominance deviations, and the various interaction deviations which contribute to the total genotypic correlation. The application of correlation in selection rests on the correlation of breeding values or the genetic correlation. It is the genetic correlation which is the cause of correlated response to selection (Mode and Robinson, 1959).

Falconer (1981), Lerner (1958) and Hallaeur and Miranda (1981) described the genetic correlation between traits as arising from either pleiotropy and or linkage disequilibrium. Pleiotropy occurs when one gene affects simultaneously several physiological pathways resulting in influence over several observed characters (Lerner, 1958). Linkage refers to genes located on the same chromosome with a tendency of being transmitted together and have not reached equilibrium frequency. Genetic or genotypic correlation, as described above is more appropriate when all genetic effects are involved (broad sense) and has a wider use in homozygous self - pollinated and in apomictic species. On the other hand, additive genetic correlation (or simply additive correlation), involving only additive gene effects, is more appropriate in cross - pollinated species (Hallaeur and Miranda, 1981).

Estimation of genetic and phenotypic correlations is based on components of variances and covariances that are estimated from analyses of variance and covariance. Covariance components are obtained in the same manner as variance components because in any experimental design, the

coefficients of expected mean products are the same as those for expected mean squares (Comstock and Robinson, 1948; Mode and Robinson, 1959).

A correlation, whatever its nature, is the ratio of the appropriate covariance to the product of the two standard deviations (Falconer, 1981). The genetic correlation then becomes:

$$rg = \frac{covg_{xy}}{(Vg_x \cdot Vg_y)^{1/2}},$$

where rg = genetic or genotypic correlation,

$covg_{xy}$ = genetic or genotypic covariance of x and y,

Vg_x = genetic or genotypic variance of x and ,

Vg_y = genetic or genotypic variance of y.

In an analysis of variance, the genotypic covariance and genotypic variance are obtained as the differences of phenotypic covariances and the environmental covariances, and the phenotypic variances and variances, respectively, so that

$$rg = \frac{cov\ P_{xy} - cov\ E_{xy}}{(VPx - VEx)^{1/2} \bullet (VPy - Vex)^{1/2}}$$

where rg = genotypic correlation,

$cov\ P_{xy}$ = phenotypic covariance of x and y,

$cov\ E_{xy}$ = environmental covariance of x and y,

VP_x = phenotypic variance of x,

VP_y = phenotypic variance of y,

VE_x = environmental variance of x and

VE_y = environmental variance of y.

Since the phenotypic covariance is the sum of the genotypic and environmental covariances i.e.

$$covP = covG + covE,$$

and the covariances can be expressed in terms of their correlations and standard deviation thus

$$covP = rpVPx^{½} \bullet Vpy^{½},$$

$$covG = rgVgx^{½} \bullet Vgy^{½}, \text{ and}$$

$$covE = r_E\, Vex^{½} \bullet Vey^{½}$$

Falconer (1981) used these relationships and showed that

$$rp = h_x\, h_y\, r_g + e_x\, e_y\, r_E\,,$$

where $h_x h_y$ = product of the square root of heritabilities of x and y,

$e_x e_y$ = product of environmental standard deviations of x and y, and

r_E = environmental correlation between X and Y (including non-additive genetic effects).

It follows that in the absence of environmental correlations, the genetic correlation can be estimated as (Falconer, 1981)

$$rg = \frac{rp}{h_x h_y}$$

The sampling variance of the genetic correlation was derived by Reeve (1955b) and by Robertson (1959b). They approximated the standard error of an estimate of rg by the following formula:

$$SErg = (1 - rg^2)\frac{(SEh^2x \bullet SEh^2y)^{1/2}}{(h^2x \bullet h^2_y)^{1/2}}$$

where SErg = standard error of the genetic correlation, and

$SE\ h^2x \bullet SE\ h^2\ y$ = product of the standard errors of the heritabilities of x and y.

2.2.4 Response to selection and its prediction

The purpose of selection is to change the population mean (Lerner, 1958). This change is termed the response to selection, symbolized by (R). Simmonds (1979) and Falconer (1981) described response to selection (R) as the difference of the mean phenotypic value between the offspring of the selected parents and the mean of the parental generation before selection. In mass selection where the selection unit is the recombinant unit, response becomes the improvement in the mean of the selected subset relative to the mean of the base population (Hallauer and Miranda, 1981).

The response or progress from selection is dependent on the average superiority of the selected parents or the selection differential (S) and also on the degree to which genotypic values of the superior parents are transmitted to offspring i.e. heritability (h^2), thus Falconer, (1981) defined response as the product of the heritabilty and the selection differential, so that:

$$R = h^2S$$

The selection differential can be standardised by dividing it by the phenotypic standard deviation (σ_p). This standardised form of the selection differential is defined as the selection intensity (i). The selection differential becomes

$$S = i\sigma_p$$

Falconer (1981) then rewrote the response prediction equation as

$$R = ih^2\sigma_p$$

If traits are additively genetically correlated, selection in the one trait will cause a change in the mean of the other trait, through the additive effects of the genes of the selected individuals (Hallauer and Miranda, 1981). Falconer (1981) described this change as the correlated response (CR) of the responding trait (Y) to the selection in the selection or primary trait (X). Falconer (1981) mathematically defined correlation response as the product of the regression of the breeding value of Y on the breeding value of X and the direct response of X so that:

$$CR = R_x b_{(A)}$$

$$= R_x \frac{cov_{(A)}\, xy}{\sigma^2_{(A)}x}$$

$$= R_x . r_{(A)} \frac{\sigma_{(A)}Y}{\sigma_{(A)}x}$$

$$= ih_x r_{(A)} \sigma_{(A)}Y, \text{ where}$$

$$R_x = ih_x \sigma_{(A)}x$$

$$= \text{direct response of the selection trait X,}$$

$b_{(A)}yx$ = regression of the breeding values of the responding trait Y on the selection trait X,

$cov_{(A)}xy$ = additive genetic covariance of X and Y,

$\sigma^2_{(A)}x$ = additive genetic variance of X,

h_x = square root of the narrow sense heritability of the selection trait X,

$r_{(A)}$ = genetic correlation of Y and X,

$\sigma_{(A)}y$ = additive genetic standard deviation of Y,

$\sigma_{(A)}x$ = additive genetic standard deviation of X,

and the rest is described as in the foregoing text .

Falconer (1981) showed how correlated response can be predicted if the genetic correlation and the heritabilities of the two traits are known since:

$CR = ih_x h_y r_{(A)} \sigma_{py}$,

Where σ_{py} = phenotypic standard derivation of Y, and the rest is defined as in the preceding sections.

2.2.5 Relative selection efficiency and the value of indirect selection.

Selection parameters include the studies of direct and indirect selection responses. The direct and indirect selections may be judged by their expected genetic gain and correlated response, respectively (Ahmad, Sharma and Khanna, 1985). Searle (1965) described how the efficiency of different methods of selection can be compared using the ratio of their responses. Where indirect selection is practised, Searle (1965) and Falconer (1981) showed that the merit of indirect selection relative to direct selection is measured by the ratio of the expected correlated response

(CR) over the direct response (R) and is defined as the relative selection efficiency (RSE) of indirect to direct selection, that is:

$$R.S.E. = \frac{CR}{R},$$

Under mass selection and where the intensity of selection is the same for the selection trait and the responding trait, the RSE of indirect to direct selection becomes (Searle,1965):

$$RSE = \frac{r_{(A)}h_x}{h_y},$$

where h_x = the square root of the narrow sense heritability of the selections trait X

h_y = the square root of the narrow sense heritabity of the responding trait Y, and the rest is defined as in section 2.2.5 above.

Searle (1965) denoted the relative selection efficiency as (p) and developed an estimate of the sampling variance of this statistic thus:

$$V(p) = [2(1+2p^2+R^2-4Rp)/h^2y+hx(1-2Rp)/2hy+p(2R\{1+2p^2-Rp\}/2-3p)]/f,$$

Where V(p) = estimate of the variance of the relative selection efficiency (p),

R = the phenotypic correlation between the selection trait X and the responding trait Y,

h^2_x = narrow sense heritability of the selection trait X with h_x as its square root,

h^2_y = narrow sense heritabilty of the responding trait y with h_y as its square root, and

f = number of parent - progeny pairs used in the estimation of the genetic covariance.

The standard errors of (p) are usually large because (p) involves the estimate h_x/h_y which can differ quite markedly for small differences in the heritability estimates (Searle, 1965). Searle (1965) and Falconer (1981) established situations when indirect selection may be preferred by setting minimum conditions of the population parameters involved in the estimation of (p).

Thus indirect selection gives speedier improvement in the genetic merit of the responding trait than does direct selection when

$$P > 1$$

i.e. $r_{(A)}h_x/h_y > 1$, and

$$h^2_x > h^2_y / r^2_{(A)} \text{ , or}$$

$$r_{(A)} > h_y$$

i.e. when the genetic correlation is greater than the square root of the narrow sense heritability of the responding trait.

2.3 Inheritance Studies

The detection of type of gene action governing the expression of a character and the estimation of the contribution of a particular component to the overall variation, are important steps in the study of inheritance of characters (Snape, 1987). Genetic analysis is useful in the formulation of effective breeding and selection strategies. In plant breeding, the knowledge of the genetic architecture of a character will determine which is the best generation in which to practise selection, what are the consequences of breeding , what are the genetic bases of heterosis and whether it is better to produce hybrids or homozygous varieties.

Genetic analyses of yield and its component traits have been conducted either on rainfed spring wheat in the subtropical regions or on hard red winter wheat in the temperate regions. This study aims to determine types of genetic variation that govern the expression of biomass yield, grain

yield, harvest index and number of tillers in a population of wheat in Zimbabwe. The irrigated spring wheat production environment in Zimbabwe is characterised by a cool vegetative period in the winter months and a warm to hot maturation phase in the early summer months. Medium to high grain yields are often obtained. Special emphasis will be made on the association of grain yield and its component traits with plant height in order to deduce the appropriateness of the height stratified selection schemes in the preceding section.

Additive genetic effects have been reported to be the major component of genetic variation in grain yield of wheat and its component traits (Batt, 1971; 1972). Dominance and epistatic effects have also been detected but were found to be of relatively minor importance (Ketata, Smith and Edwards, 1976; Paroda and Joshi, 1979). In a later study conducted on two spring wheat crosses by Srivastava, Sharma and Yunus (1992), additive gene effects for grain yield per plant were significant in both crosses and were also higher in magnitude than interactive gene effects. This result was similar for grains per ear and for 1000 - grain weight. Dominance effects were higher than additive effects for biological yield per plant in one of the crosses and also for tiller number per plant for the other cross. The genetic basis of heterosis for biological yield per plant and tiller number per plant is thus dependent on the cross. All traits showed the presence of epistasis in this study. In certain instances, single plant measurements may inflate the environmental variances resulting in masking of the genetic effects. This occurred in the inheritance study of Sidwell, Smith and McNew (1976) in which the additive and dominance variances were non significant relative to the environmental variances for tiller number per plant, grain yield per plant and other kernel characteristics except for kernel weight which showed high narrow sense heritability.

The inheritance of harvest index was studied in several wheat crosses by Batt (1976) who found large additive gene effects in all the crosses and relatively minor non-additive gene effects in

some of the crosses. There was complete absence of high parent heterosis for harvest index but mid parent heterosis was found in all the crosses.

Since additive genetic variance formed the major part of the genetic variance for yield and its component traits with evidence of presence of some dominance and epistatic effects, wheat scientists have suggested the use of intermating of selects followed by visual selection in early segregating generations. This simultaneously exploits both types of gene effects. Further, this approach is likely to break some undesirable linkages, resulting in the establishment of rare useful recombinations (Srivastava, Paroda, Sharma and Yunus, 1989).

In this study the detection and estimation of gene effects will be conducted using the generation mean analysis suggested by Mather and Jinks (1971). Hallauer and Miranda (1981), Snape (1987) and Mashiringwani (1993) outlined the appropriateness of the generation mean analyses in inheritance studies in wheat, noting the relative ease with which the selfing generations can be raised. Sampling errors are inherently smaller in the generation mean analysis than in the estimation of genetic variances because means are first order statistics while variances are second order statistics which contain squared terms. In the generation mean analysis all the genetic effects including epistasis can easily be detected using relatively simple experiments. These authors, listed the failure of estimation of heritability as one of the major disadvantages of the generation mean analysis. Other limitations of the generation mean analysis were described by Hayman (1960) for the digenic epistatic model that includes epistatic effects.

It is only in the absence of epistatic effects that the estimates of additive and dominance genetic effects are meaningful and unbiased by linkage disequilibrium. If epistatic effects are present, estimates of additive and dominance genetic effects are biased by epistatic effects and linkage

disequilibrium. Since the generation mean analysis does not reveal opposing effects, cancellation of effects may be a serious disadvantage: For example dominance effects may be present but opposing at various loci in the two parents and thus cancel each other.

2.3.1 Detection of type of gene action

Mather and Jinks (1971) presented some simple relationships between means of generations derived from the F1 of a cross between two homozygous parental genotypes as shown below.

F2 = 1/4P1 + 1/4P2 + 1/2F1

B1 = 1/2P1 + 1/2F1

B2 = 1/2P2 + 1/2F1

where F2, B1 and B2 are the second filial generation, the backcross of F1 to the first parent and the backcross of the F1 to the second parent, respectively. These predicted relationships are only valid in the absence of non allelic interaction, equal viability and fertility of individuals in all the generations and when either additive gene effects, dominance effects or both additive and dominance effects are the only cause of genetic variation (Mather, 1949).

Earlier on Mather (1949) drew up expectations of the generation means which fit the additive dominance effects model known as the individual scaling tests i.e.

A = 2B1 - P1 - F1

B = 2B2 - P2 - F1

C = 4F2 - 2F1 - P1 - P2

D = 2F2 - B1 - B2

Each of these equations is expected to equal zero if the additive - dominance model adequately describes the variation between the means of the basic generations. The quantities A, B, C and D

will not be exactly equal to zero, even if the genes controlling the character display additive and dominance effects only, because the family means from which they are derived will be subject to sampling variation. Mather (1949) gave the sampling variances of the individual scaling tests as the sum of the variances of generations involved e.g.

VA = 4VB1 + VP1 + VF1

The number of degrees of freedom attached to these sampling variances is obtained by summing the degrees of freedom of the generation involved; that is, the degrees of freedom of VA are:

NB1 + NP1 + NF1

where N = number in the generation.

The ratio $A/(VA)^{1/2}$ can be treated as a normal deviate when the number of degrees of freedom of the sampling variance is greater than 30, or as t, when this number is smaller than 30. The D scaling test provides a test mainly of the additive x additive type of gene action, the C scaling test of the dominance x dominance type of epistasis and significance of both A and B scaling tests indicates the importance the of the additive, additive x dominance and dominance x dominance types of gene action (Mashiringwani, 1993).

2.3.2 Estimate of gene effects using generation means.

The individual scaling tests merely detect presence or absence of the additive and/or dominance genetic effects assuming non - allelic interaction. Moreover these scaling tests are not very accurate since they are not statistically independent and variable in precision of estimation. Individual generations appear in more than one equation. Estimates of the contribution of the additive genetic variance and that of the dominance genetic variance can be obtained using the joint scaling test procedure proposed by Cavalli (1952). These estimates are unique only in the

absence of non - allelic genetic variation. In this additive - dominance model, three parameters are estimated from the generation means viz

m	=	mean of the two parental genotypes,
[d]	=	additive genetic variance component and
[h]	=	dominance genetic variance component.

These estimates of the parameters of the model are fitted to the data by the weighted least squares procedure. The significance of each of the parameters can be tested using its own standard error (Mather and Jinks, 1971). The sums of squares of the differences between the observed and expected values of the mean for each generation yields a goodness of fit chi-square test which can be used to test the adequacy of the model, provided that the number of parameters in this model is less than the number of equations or generations (Cavalli, 1952; Mather and Jinks, 1971). The degrees of freedom for this test is G - P where G is the number of generations and P is the number of parameters fitted (Mather and Jinks, 1971).

If the chi-square testing the goodness of fit of the model to the data is significant, it means that the additive - dominance model is inadequate and that this failure of the model may be due to the effects of linkage, epistasis or both (Anderson and Kempthorne, 1954; Hayman, 1986b; Mather, 1949; Mather and Jinks, 1971).

Models for estimating different genetic components of epistatic variance were proposed by Anderson and Kempthorne (1954) and Hayman (1958b) and subsequently by Mather and Jinks (1971). In the specification of full digenic epistatic model, Mather and Jinks (1971) stipulated the

requirement of a minimum of six generations for a perfect fit solution. The three digenic epistatic components specified are as follows:

[i] = pooled additive x additive epistatic effects,

[j] = pooled additive x dominance epistatic effects,

[l] = pooled dominance x dominance epistatic effects.

Failure in the fit of the digenic epstatic model may indicate presence of linkage, higher order non - allellic interaction or both (Hayman, 1985b; Mather and Jinks, 1971).

The detection of linkage of genes showing digenic interaction was again outlined by Mather and Jinks (1971). The specification of parameters in this model is eight, requiring ten generations in their estimation, leaving two degrees of freedom for testing the goodness of fit of the model. Higher order interactions and linkage can be confounded leading to the failure to detect higher order interactions (Mashiringwani, 1993). Jinks and Perkins (1969) described a procedure for distinguishing between the effects of linkage and higher order epistasis in generation means.

Genotype x environment interactions relative to gene effects can be estimated by fitting the model by Mather and Jinks (1971) i.e.;

$$P = m+[d] + [h] + [i] + [j] + [l] + e$$

where e = environmental effects and the other parameters are as defined above.

Adequacy of this model indicates absence of genotype x environment interaction. Inadequacy of the above model leads to the next stop, that of estimating genotype x environment interaction for each genetic effect by the non genotype x environment interaction model here defined after Mather and Jinks (1971) as:

P = m + [d] + [h] + [I] + e + gd + gh + gi + gj + gl;

where gd = interaction between environment and additive genetic effect;

gh = interaction between environment and dominance genetic effects;

gi = interaction between environment and additive x additive genetic effects;

gj = interaction between environment and additive x dominance genetic effects;

gl = interaction between environment and dominance x dominance genetic effects.

Additive genetic effects have generally been found to be the most stable across environments (Hayman, 1958b; Gamble, 1962; Sun, Shands and Forsberg, 1972). Non - additive genetic effects were relatively more variable across environments (Rojas and Sprague, 1952).

2.3.3 The nature and estimation of heterosis

Heterosis is defined as the superiority of the F1 over the mid - parent value (mid - parent heterosis) (Ansori Rajper, Dharejo, Malik and Ansari, 1989; Stransfield, 1983) or in practical breeding, superiority of the F1 over the better parent (better parent heterosis) (Mather and Jinks, 1971). Analysis of the cause of heterosis is essential in assessing the probability of obtaining pure breeding lines as good as or better than the F1 and so whether it is better to produce hybrids or

pure breeding lines (Frankel, 1983; Snape, 1987). Mather and Jinks (1971) showed that positive or negative heterosis occurs when the absolute value of the pooled dominance effects [h] is greater than the value of the pooled additive effects [d]. For $\pm$ [h] to be greater than [d] one or both of the following conditions must be satisfied (Mather and Jinks, 1971):

(i) The net value of the heterotic loci (hi) must be greater than the net value of the additive loci (di), that is there must be over dominance ($hi/di > 1$) at some or all loci.

(ii) The coefficient of association of increasing or decreasing alleles between the two parents (rd) must be less than one ($rd<1$) and approaching zero, to produce heterosis, i.e. there must be dispersion of completely ($hi = di$) or incompletely dominant genes ($hi<di$).

In addition, heterosis is more likely to occur if the signs of all the dominant loci are the same, i.e. dominance is unidirectional with the consequence that [h] is not reduced by the external cancellation of dominant loci of different signs.

Mid - parent heterosis is given by F1 - ½ (P1 + P2) and better parent heterosis is F1 –P1 where P1 is the better parent. The statistical significance of heterosis can be tested using the parent versus F1 by family interaction as error (Matzinger, Wernsman and Ross, 1971). Alternatively, a t - test can be used to compare F1 means with mid - parental values (Wynne, Emery and Rice, 1970). The expression of hybrid vigour or heterosis can be influenced by the environment (environmentally dependent heterosis) and may be also subject to genotype x environment interaction (Frankel, 1983). It is therefore necessary to measure heterosis in yield and its component characters under Zimbabwean cultural conditions.

3. MATERIALS AND METHODS

3.1 Experimental sites and management of trials

The experiments were conducted at two research station sites and also on one commercial farm site. These three sites are situated in the high- yielding environment for wheat production in Zimbabwe. These sites are very uniform in soil texture and fertility. The Rattray Arnold Research Station (RA) and ORIBI commercial farm (ORIBI) are located in the middleveld areas at altitudes 1 300m and 1 250m above sea level, respectively. The respective, exact locations for the two sites are 17^{o}40'S, 31^{o}14'E and 17^{o}37'S, 31^{o}24'E. About 70 percent of the Zimbabwean wheat is produced in the middleveld areas. The bulk of the remainder is produced in the lowveld areas (<900m), with only about 10 percent being produced in the highveld (> 1 250m above sea level). The soils at RA and ta ORIBI farm belong to the Salisbury 5E2 Series (Verboom, 1980), and are dark reddish brown with clay contents ranging from 40 to 45 percent in the top soil and 40 to 60 percent in the subsoil. Soil pH in the top soil ranges from 5 to 6 on the calcium chloride scale. The third site which represented the highest wheat yield potential environments in Zimbabwe, is the Agricultural Research Trust farm (ART) located at latitude 31^{o}5'E and longitude 17^{o}43S, at an altitude 1530m above sea level. The soils at ART Farm are also predominantly red clays of fersiallitic type derived from epidiorite Salisbury 5E2 series.

All the experimental sites were fertilized for optimum growth of wheat that is produced in the winter months under irrigation. Luxurious amounts of basal compound fertilizer 'Z' (8%N: 14%P_2O_5: 7%K_2O) were applied at 500kg ha^{-1}. Nitrogen top dressing was in the form of Ammonium Nitrate (34,5%N) at the rate of 400 kg ha^{-1} in two equal splits: the first nitrogen top dressing was applied within the third week after planting, the second nitrogen application was done at six weeks after planting.

The highly selective herbicide, ALLAY 20DF (metasulfuron-s-methly), was applied at 20 g ha^{-1} to control maize (*Zea mays* L.) and soyabean (*Glycine max* L.) volunteers and a wide range of broad leafed weeds. The wheat experiments were grown within a soya – wheat rotation.

Frequencies of irrigation were based on the irrigation schedule designed by MacRobert (1993). The total amount of irrigation water applied at RA in 1993 was 570mm. The irrigation water applied at RA, ART and ORIBI in 1994 was 580mm, 560mm and 490mm, respectively. Incidence of diseases and pests was negligible in all the field experiments. Diurnal temperature range during the vegetative phases (May – July) was 4,5^{o}C minimum, to 23,1^{o}C maximum. The temperature range during the flowering and early grain filling period (August – September) was 6,7^{o}C minimum, to 26,4^{o}C maximum. The late grain filling period and maturation times were characterised by sharp rise in temperatures ranging between 13,0^{o}C minimum and 29,9^{o}C maximum.

3.2 Evaluation of Selection Criteria

Three attributes of single ear -to -row progenies were considered for application as auxiliary characters for selecting high grain yielding genotypes of wheat viz; biomass of the whole single ear-to-row progeny, earmass of the whole ear- to- row progeny and harvest index of the whole single ear-to-row progeny. These traits were measured as described in section 3.2.2.

3.2.1 Spring wheat crosses used in the selection and their constituent parents

Six bi-parental crosses among elite spring wheat lines were made in winter 1990 at the Rattray Arnold Research Station. They were advanced for further generations, to the F3 generation, by growing the F1 generation in the summer, in the green house at Rattray Arnold Research Station (RA). The F2 generation was also grown at RA, but in winter, while the F3 generation was grown during summer at Warwick farm in Marondera (1580m above sea level, 18° 10' S 31° 30' E). The populations generated from the bi-parental matings are listed below

Population 1 (P1) = Sengwa x Nata

Population 2 (P2) = Sengwa x CP19/83/6/5

Population 3 (P3) = Sengwa x CP105/83/6/22

Population 4 (P4) = Nata x CP9/83/5/2L

Population 5 (P5) = Nata x CP105/83/6/22

Population 6 (P6) = Nata x CP16/83/6/2

The recurrent parents, Sengwa and Nata are medium to high grain yielding spring wheat cultivars which have been grown extensively in Zimbabwe. Sengwa is a short to medium statured commercial variety, being 75-80cm tall and has a high HI. Nata is a tall statured variety with plant height ranging between 90cm and 95cm, and has high biomass and grain yield potential. The remainder were adapted experimental lines that were selected from breeding populations originating from the International Maize and Wheat Improvement Centre (CIMMYT) in Mexico.

Agronomic characteristics of the parents used in the bi-parental matings of the above six wheat populations are presented in Table 3.1

Table 3:1: **Agronomic characteristics of six wheat varieties constituting the parents of the six bi-parental crosses at an altitude of 1300m**

Variety	Grain yield (t/ha)	Days to anthesis	Days to maturity	Biomas grams/0,9m² Row(A)	Earmass grams/0,9m² Row(B)	Harvest Index % (B/A)	Plant Height (cm)
Sengwa	9,3	89	152	1257	625	51	75
Nata	9,6	92	154	1326	747	45	92
Cp105/83/6/22	9,9	90	155	1401	693	49	90
Cp19/83/6/5	9,7	88	153	1291	648	50	88
Cp9/83/5/2L	9,5	93	156	1320	661	50	93
Cp16/83/6/2	9,1	95	155	1492	686	46	94

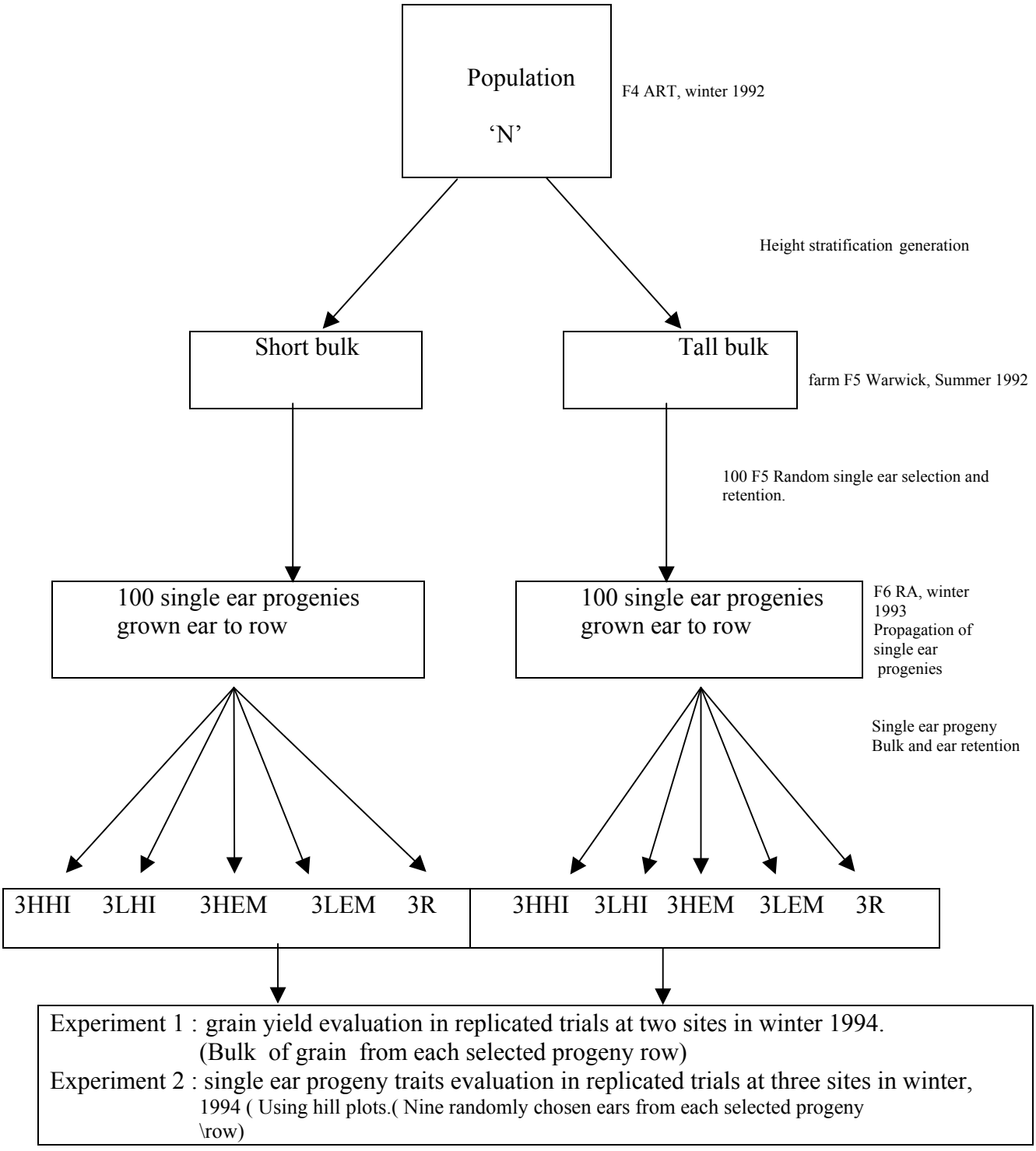
3.2.2 Sampling and selection procedure

The six breeding populations were expected to be homozygous for genes controlling plant height at the F4 generation, since the mode of inheritance of this trait is predominantly additive (Johnson, Biever, Haunold and Schimdt, 1966). Random selection of ears in the two plant height strata, the short height stratum (85cm) and the tall height stratum (>85cm), was conducted at this fourth final generation of the six populations at ART in winter 1992. Bulks of the short or tall statured sub-populations were advanced a further generation during the following summer 1992 at Warwick farm in Marondera. In winter 1993, 100 single ears which had been randomly selected from each of the twelve sub-populations, and also from each of the six parents were individually grown at RA in rows, 1,5m long and 0,6m apart. A pathway, 0,5m wide separated the ends of the single-ear progeny plots. Nine single ears from each single ear-to-row progeny

within each subpopulation or parent, were retained at maturity during the month of October 1993.These were reserved for future use in the replicated evaluation of single ear progeny attributes planned for the following winter 1994.

The remaining single ear-to-row progenies were individually cut manually at ground level using a sickel and subsequently air-dried. Total biomass of each single ear progeny was subsequently measured. Ears were snapped off at the neck of the peduncles and then weighed for each single ear-to-row progeny: This attribute was recorded as 'earmass'. Harvest index or the ratio of earmass to biomass, was in turn calculated for each of the 100 single ear to row progeny from each subpopulation.

The three attributes measured in all the single ear progenies were ranked in order of magnitude. Three top ranking progenies and three lowest ranging progenies, plus three randomly selected single ear progenies were sampled for each of the twelve height stratified sub-populations. It was noted that biomass and earmass were very strongly positively correlated (r>0,8). Thus the top or bottom three selects for these attributes finally represented both attributes. Selection on biomass or earmass and harvest index was by independent culling levels as described by Lerner (1958) and Baker (1987). The selected single ear progenies of each sub-population and those of the constituent parents, and the nine single ears derived from each of them, were subjected to replicated statistical field evaluation in the following winter, 1994. A flow chart of the selection and field evaluation procedure is presented in Fig.1 which follows.



Where HHI = High harvest index
LHI = Low Harvest index
HEM = High biomass or earmass
LEM = Low biomass or earmass
R = Random selection

Fig. 1: Flow chart of wheat selection and testing procedure adopted in the study.

3.2.3 Evaluation of the responding trait; grain yield, and the auxiliary traits; biomass, earmass, harvest index and plant height of single-ear progenies

The three single ear progeny bulks retained for each of the selection criteria and also bulks of the constituent parents of each population, were grown in experiments at two sites (ART and RA). The grain yield field evaluation was designated as Experiment 1 and was confined to the two sites because the amount of seed was limiting. Experiment 2 was conducted at three sites (ART, ORIBI and RA) and comprised entries from the nine single ears retained for each of the selected single ear-to-row progeny and also from each of the constituent parents. The two experiments are described below.

3.2.3.1 Experiment 1: Evaluation of grain yield and estimation of its heritability

The seed retained from each of the selected single ear-to-row progenies grown in winter 1993, was drilled using a ten-row planter. The seeding rate used was 100 kilograms of seed per hectare. The trials were planted in early May 1994 at RA and ART. For each population, the thirty selections plus its constituent parents were laid in a Randomised Complete Blocks Design with two replications at each site. The selection treatments are described in Table 3.2. Each population constituted a separate trial and the trials were laid adjacent to one another at each site. Gross plot size was ten rows of 6m in length and 0,2m apart, which was later reduced to a length of 5,5m to accommodate a 50cm pathway between the ends of the plots.
The harvested net plot area was 6.6m². The plots were reaped at maturity during October of the same year. A Hege 125 plot combine which reaps the centre 6 rows of each plot, was used for harvesting the trials.

The following measurements were recorded for each plot:

Days from planting to anthesis: When 50% of the culms had protruding anthers,

Days from planting to maturity: When 95% of peduncles were fully ripe or had just turned yellow in colour,

Per cent lodging: A visual estimate of the number of plants leaning over more than 45^{o} within the $6,6m^2$ net plot area at maturity,

Plant height: Measured from soil level to the tips of the ears of upright plants in cm,

Seed yield: Mass of seed per plot in grams and

Grain Moisture: Per cent moisture of seed to the nearest 0,1% at weighing.

Table 3.2 Selection treatments evaluated in experiment 1 and 2 for each of the six wheat populations (P1 – P6)

Entry No.	Selection criteria	Plant Stature
1 –3	High biomass or earmass	Short height
4 – 6	Low biomass or earmass	"
7 – 9	Random	"
10 – 12	High harvest index	"
13 – 15	Low harvest index	"
16 – 18	High biomass or earmass	Tall height
19 – 21	Low biomass or earmass	"
22 – 24	Random	"
25 – 27	High harvest index	"
28 – 30	Low harvest index	"
31 – 32	Parent 1 and 2	

3.2.3.2 Statistical analysis of grain yield data from experiment 1

The accessions (i.e. selections) and parents of each cross were evaluated in separate trials at each of the two sites.The Randomised Complete Blocks design analyses at a single site and over the two locations, were conducted according to the following models:

For the single site analysis of the model according to Montgomery (1976), was

$Y_{ij} = u + G_i + R_j + E_{ij}$

Where, Y_{ij} = is the i^{th} observation in the j^{th} replicate

u = the mean of the genotypes over all replicates

G_i = the effect of the i^{th} genotype

R_j = the effect of the j^{th} replicate, and

E_{ij} = the random error effect associated with the ij^{th} observation.

The ANOVA across sites followed the model similar to that applied by Atlin and Frey (1989) i.e.

$Y_{ijk} = u + G_i + L_j + (GL)_{ij} + R/L_{k/j} + E_{ijk}$

where Y_{ijk} = is the k^{th} observation in the j^{th} replicate of the i^{th} location,

U = overall mean of the genotypes,

G_i = effect of the i^{th} genotype,

L_j = effect of the j^{th} location,

$(GL)_{ij}$ = the interaction effect of the i^{th} genotype and the j^{th} location,

$R/L_{k/j}$ = effect of the k^{th} replicate in the j^{th} location, and

Eijk = the pooled random error effect associated with the i^{th} genotype in the j^{th} location in the k^{th} replicate.

Algorithms of the expected mean squares in the analyses of variance (after Montgomery, 1976) of grain yield data at one location and across the two locations, are presented in Tables 3.3 and 3.4 respectively.

Table 3.3: E(ms) algorithms for grain yield of 32 genotypes in an RCBD, 2 reps at 1 location

Factor	DF	Effect	E(ms)	Mean Square Symbol
		R R		
		G r		
		I j		
B_j	r – 1 (1)	G 1	$a\sigma^2_B + \sigma^2_E$	M3
G_i	g – 1 (31)	1 r	$r\sigma^2_G + \sigma^2_E$	M2
Eij	(g – 1)(r – 1) (31)	1 1	σ^2_E	M1
Total	rg –1 (63)			

Classification of factors are as follows:

B_j = replicate, random (R) j = 1, J,

G_i = genotypes, random (R), i= 1, I and

E_{ij} = pooled random error.

Table 3.4: E(ms) algorithms for grain yield of 32 genotypes in an RCBD, 2 reps at 2 locations

Factor	DF		Effect			E(ms)	Mean Square Symbol
			R	R	R		
			l	g	r		
			j	i	k		
L_j	(l – 1)	(1)	1	g	r	$rg\sigma^2_L + g\sigma^2_{B(L)} + \sigma^2_E$	M5
G_i	(g – 1)	(31)	1	1	r	$rl\sigma^2_G + r\sigma^2_{GL} + \sigma^2_E$	M4
GL_{ij}	(g – 1)(l – 1)	(31)	1	1	r	$r\sigma^2_{GL} + \sigma^2_E$	M3
$B_{(j)k}$	l(r-1)	(2)	1	g	1	$g\sigma^2_{B(L)} + \sigma^2_E$	M2
$E_{(ij)k}$	l(r – 1)(g – 1)	(62)	1	1	1	σ^2_E	M1
Total	lgr - 1	(127)					

Classification of factors is as follows:

L_j = location, random (R), l x g, j = 1, L,

G_i = genotypes, random (R), I = 1, G,

$B_{(j)k}$ = replicate within location, random (R), b(l), g x b, k = 1, k and

$E_{(ij)k}$ = pooled random error.

Variance components were estimated by equating mean squares to their expectations (Pixley and Frey, 1991). The Expected mean square (E (ms)) statistic is a ratio of mean squares chosen so that the expected value of the numerator mean square differs from the expected value of the denominator mean square only by the variance component of interest (Montgomery, 1976). Standard errors for the components of variance were calculated according to the method of Anderson and Bancroft (1952) and of Comstock and Moll (1963). Entry mean heritabilities which estimated broad-sense heritabilities (H^2), were estimated using components of variance as outlined by Hallaeur and Miranda (1981), recognising that;

$$H^2 = \sigma^2_G/\sigma^2_P$$

$$= \sigma^2_G\,(\sigma^2_E/rl + \sigma^2_{GL}/l + \sigma^2_G)^{-1}$$

Where, σ^2_E = pooled error variance,

σ^2_G = genotypic variance,

σ^2_{GL} = genotype x location interaction variance,

r = number of replications and

l = number of locations.

Since the genotypic variance σ^2_G is here represented by (M4 – M3)/rl, and the phenotypic varience σ^2_P is represented by M4/rl it follows that the entry–mean heritabilities (H^2) above, were estimated as M4 – M3/rl ÷ M4/rl i.e. ;

$$\sigma^2_G/\sigma^2_p = 1 - M3/M4\ .$$

The interaction mean square (M3) was used in the estimation of h^2, even in the ANOVA of the populations in which it was nonsignificant in order to remove upward bias due to its presence.

Standard errors of these heritabilities were computed according to Hallaeur and Miranda (1981) after Comstock and Moll (1963) formula:

$$SE(h^2) = \frac{SE(\sigma^2_G)}{\sigma^2/(rl) + \sigma^2_{GL}/l + \sigma^2_G}$$

Where SE = standard error, and the rest is defined as in section 3.2.3.2. The standard error of σ^2_G was obtained from Table 3.4 as the square root of

$$\frac{2}{(rl)^2}\left[\frac{M^2_4}{n+1} + \frac{M^2_3}{(l-1)(n-1)+2}\right]$$

Where n = number of accessions and the rest is defined in section 3.2.3.2. Confidence intervals (90%) for heritabilities were computed as suggested by Knapp *et al.* (1985)

The entry-mean heritabilities were later used as narrow- sense heritabilities following the deductions of Hanson (1963) and Dudley and Moll (1969) that in the evaluation of homozygous lines, the genotypic line component of variance estimates the additive genetic variance. Bias in the estimates of narrow - sense heritability in this way would only arise from additive x additive epistatic genetic variance and also from inadequate sampling of the environmental variance.

In mass selection, genetic advance is a function of the genetic coefficient of variation (G.C.V), the selection differential and the heritability in the narrow sense (Johnson, Robinson and Comstock, 1955). In these selection studies, the genotypic variances in the different crosses , different plant height strata and different selection attributes were compared on `relative terms using the genetic coefficient of variation, which was calculated as follows;

G.C.V = (genotypic variance)$^{-1/2}$ / mean of genotypes * 100

Comparisons of the different selection criteria were conducted using the between – group and within – group orthogonal contrasts as defined by Gomez and Gomez (1984). Means were compared using the mean separation method specified by the Duncan's Multiple - Range test (Little and Hills, 1978) which gives the statistically significant differences between means as;

D = R (LSD) where ;

D = the difference between the means,

R = the tabular value from Table 4.4 of Little and Hills (1978) for testing means at various ranges at the 5% level of probability for given degrees of freedom for "error"and

LSD = the least significant difference of the means.

3.2.3.3 Experiment 2 : Evaluation of single- ear progeny traits; biomass, earmass, HI and plant height

The determination of relative selection efficiencies of the morpho-physiological traits of single-ear progenies , biomass, earmass, HI and plant height required the establishment of their heritabilities, their mutual associations and their respective associations with grain yield. Thus the nine single ears retained for each selected accession and also from each of the parents, were grown in winter 1994 in statistically designed experiments at three sites.

Using the same micro or hill plot dimensions as described for winter 1993 (see section 3.2.2), seed from individual ears was planted in hill plots in winter 1994, at three sites, RA, ART and ORIBI. Three single progeny plots were planted from each selected accession or parent at each site. The thirty accessions and 2 parents reaped from single ear progenies of population were

arranged in randomised complete blocks design with three replicates per population, per location. The selection criteria treatments were exactly the same as in Experiment 1. Plant biomass, earmass (mass in grams of all ears reaped from each single ear progeny), HI and plant height, were recorded for each single ear progeny. The ANOVA for each single ear progeny trait and the subsequent estimations of heritability on an entry- mean basis were conducted in exactly the same manner as in Experiment 1 (Section 3.2.3.2).

3.2.4 Associations between grain yield measured in Experiment 1 and single-ear progeny traits measured in the previous winter, 1993

Phenotypic correlation coefficients (rp) between means of either biomass, earmass, or HI, which were measured in single ear-to-row progenies, and grain yield of the corresponding accessions derived from the respective single ear progenies, were calculated using Pearson's product moment correlation method. Corresponding genotypic correlation coefficients (rg) were calculated according to Falconer (1981). In the absence of environmental correlations as was the case in these relationships, Baker (1987) and Falconer (1981) gave an estimate of genotypic correlation in terms of the phenotypic correlations and the heritabilities of the characters as:

$$rg = rp / h_x h_y$$

where,

rg = genotypic correlation coefficient between character x and character y,

rp = the phenotypic correlation coefficient between the two characters,

h_x = the narrow sense heritability of character x,

h_y = the narrow sense heritability of character y.

The standard error of the estimate rg was computed after Reeve (1955b) and Robertson (1959b) as described in section 2.2.3.

3.2.5 Associations among single-ear progeny traits, biomass, earmass, HI and plant height

Phenotypic and genotypic correlations were estimated for the relationship among single ear progeny traits, biomass, earmass, HI and plant height as the ratios of the appropriate covariances to the product of the respective standard deviation i.e. according to Falconer (1981) phenotypic correlations were estimated. Thus the phenotypic correlations were estimated from the total phenotypic covariance and variance line and the genotypic correlations, from the genotypic covariance and variance line in the analysis of variance and covariance using the statistical software package, Minitab Release 7.2.

3.2.6 Relative Selection Efficiency (RSE) of single-ear progeny traits; biomass, earmass and HI in the indirect selection for grain yield ability

The efficiency of using either biomass, earmass or HI of single ear to row progenies as selection traits for high grain yield performance relative to direct selection for grain yield in grain yield trials was estimated following the methods of Searle (1965) and Falconer (1981). The relative efficiency (RSE) of the selection trait (x) is the ratio of the correlated response from indirect selection to the direct response of the responding trait (y) so that

$$RSE = rgh_x/h_y$$

Where h_x = square root of the narrow sense heritability of the selection trait, and

h_y = square root of the narrow sense heritability of the responding trait.

The statistical significance of the estimate of RSE was tested using its standard error estimated after Searle (1965) (see section 2.2.5).

3.3 Inheritance studies : Experiment 3 :

The inheritance of biomass, earmass, harvest index and number of tillers of individual plants, were studied in the spring wheat cross Sengwa x Nata. The spring wheat variety Sengwa is short statured and possesses high harvest index. The other parent, Nata is a tall statured spring wheat variety which possesses high biomass and high grain yield (see Table 3.1). The inheritance of plant height was also included in the study with special emphasis on the association of plant height with the three selection criteria, biomass, earmass, and HI and also productive tillers.

3.3.1 Mating design and field experiments

The genetic studies were conducted using the six populations of the above cross, *viz*; parent one (P1), parent two (P2), the first filial generation (F1), the first backcross generation of P1 onto F1 (BC1), the first backcross generation of P2 onto F1 (BC2) and the second filial generation (F2).

Two hundred and forty single plants of each population were planted in May 1994 using plots which were 6 rows, 4m long and 40cm apart. Distance between single plants in the row was 10cm. A total of three such plots per family were planted at each of the two locations, ART and ORIBI. Thus the six families were laid in Randomised Complete Blocks design with three replicates at each site. Plant height measurements of the plants within the central 3m length of each of the four inner rows, was recorded. The same plants of each plot were later manually cut at ground level when they were completely dry in late October of the same year. Biomass, earmass and HI were recorded in a similar manner to that performed in Experiment 2 in section 3.2.3.3 for single ear progeny plots. The number of productive tillers per plant was also recorded.

3.3.2 Estimation of gene effects using generation means

The adequacy of the additive–dominance genetic effects model which nulls any other sources of genetic variation, was tested using the A, B, C and D individual scaling tests proposed by Mather (1949) as outlined in Section 2.3.1 of this thesis. These tests were conducted using generations grown at each of the two sites. The non epistatic model was also tested over generation means of the two sites using the joint scaling test according to Mather and Jinks (1971). This test also included the environmental and interaction effects terms. The goodness of fit of this model was tested using a Chi-square test with six degrees of freedom. A digenic epistatic model which included the additive x additive (i), the additive x dominance (j) and the dominance x dominance (l) epistatic genetic effects was also fitted for individual sites after Mather and Jinks (1971).

These were perfect fit models with no degrees of freedom remaining to test their goodness of fit. In addition, the full digenic epistatic model which included the environmental effect (e), was fitted to the data across locations in order to determine the relative importance of the environmental effects for the five characters in the wheat crop. The goodness of fit of this non genotype x environment interaction model was tested using the Chi-square test with five degrees of freedom. The t-test was used for testing the significance of individual estimates of genetic and environmental effects. The full digenic epistatic model which assumes presence of genotype x environment interaction was finally fitted to ascertain the genotype x environment interaction effects. This was another perfect fit model in which only the significance of individual estimates was tested by the t-test.

All the genetic and environmental parameter estimates and their standard errors were obtained from the solutions of the matrix (Fischer, 1946; Searle, 1966).

$$M = J^{-1}S$$

Where, M = matrix of estimates

J^{-1} = inverse of the variance - covariance information matrix (J), and

S = scores matrix

The standard errors of the estimates were obtained as the corresponding diagonal elements of the M matrix. The Genstat 5 release 2.2 statistical software of the Lawes Agricultural Trust (Rothamsted Experimental Station, U.K.) Copyright 1990, was used to determine the solutions of the matrices.

3.3.3. Estimation of heterosis

Heterosis for each character was calculated as the increase in F1 performance over the mean parental and better parental performances in experiment 3.

A t-test formula given by Wynne, Emery and Rice (1970) was used to ascertain the significance of the estimated values of heterosis as follows

$$T = [F1_{ij} - MP_{ij}]/[3/8\ (S^2E)^{½}MP_{ij}],$$

Where $F1_{ij}$ = the mean of the ij^{th} F1,

MP_{ij} = the mid-parental value for the ij^{th} cross, and

S^2E = the estimate of error variance.

3.3.4. Estimation of heritabilities

Broad sense (H^2) and narrow sense (h^2) were estimated for each character at each of the two sites according to Nyquist (1991) after Warner (1952) i.e.

$$H^2 = \frac{\sigma^2_{F2} - [(\sigma^2_{P1} + \sigma^2_{P2} + 2\sigma^2_{F1})/4]}{\sigma^2 F2}$$

$$h^2 = \frac{[2\sigma^2_{F2} - (\sigma^2_{BC1} + \sigma^2_{BC2})]}{\sigma^2_{F2}}$$

Where σ^2_{F2} = phenotypic variance of the F2 population,

σ_{2F1} = phenotypic variance of the hybrid F1,

σ_{2BC1} = phenotypic variance of the first backcross of P1 onto F1,

σ^2_{BC2} = phenotypic variance of the first backcross of P2 onto F1,

σ^2_{P1} = phenotypic variance of parent 1, and

σ^2_{P2} = phenotypic variance of parent 2.

The standard error of h^2 was determined after Ketata, Edward and Smith (1976) as modified by Nyquist (1991) as the square root of the variance of heritability as follows:

$$\sigma^2_{h^2} = 2(a + b + c)/(\sigma^2_{F2})^2$$

Where $a = (\sigma^2_{BC1} + \sigma^2_{BC2})^2/(df_{F2+2})$,

$b = (\sigma^2_{BC1})^2/(df_{BC1+2})$ and

$c = (\sigma^2_{BC2})^2/(df_{BC2+2})$.

A pseudo F (F^1) test was then conducted to test whether the additive variance and the heritability equalled zero, as follows:

$$F1 = 2(\sigma^2_{F2})/(\sigma^2_{BC1} + \sigma^2_{BC2})$$

with the numerator degrees of freedom (df1) = df_{F2} and degrees of freedom (df2) as follows:

$$df2 = \frac{(\sigma^2_{BC1} + \sigma^2_{BC2})^2}{[(\sigma^2_{BC1})^2/df_{BC1} + (\sigma_{2BC2})^2/df_{BC2}]}.$$

3.3.5. Association of single plant characters

The mutual association of all the five characters measured in single plants including the pertinent relationships with plant height, were determined using the covariances and variances of the appropriate generations of the cross. Both the phenotypic correlation coefficients (rp) and genotypic correlation coefficients (rg) were calculated following Johnson, Biever, Haunold and Schmidt (1966) method as follows:

$$rp_{xy} = \frac{\text{covariance } XY_{F2}}{[(\text{variance } X_{F2})(\text{variance } Y_{F2})]^{1/2}}$$

$$rg_{xy} = \frac{\text{covariance } SY_{F2} - \text{covariance } XY_{F1}}{[(\text{var.}X_{F2} - \text{var.}X_{F1})(\text{var.}Y_{F2} - \text{var. } Y_{F1})]^{1/2}}$$

where x and y are the two characters being correlated. Significance of these correlation coefficients were tested using tabular r values in Fisher and Yates (1918) statistical tables.

4. RESULTS

4.1 Results of experiment 1: Grain yield data

4.1.1 Grain yield performance of the genotypes of six spring wheat populations

Separate analyses of variance combined over the two sites (ART and RA), for each of the six wheat populations, are presented in Table 4.1. Grain yield performance of wheat genotypes (i.e. accessions and parents) was similar at both sites except for populations 2 and 4. Statistical significance of the block mean square shows that blocking was effective in local control of residual variation in five out of the six populations. In turn, the statistical significance of the accession mean squares in the unstratified populations and also in the short height and tall height strata rendered scope for comparison of efficiency of the different auxiliary traits in the selection for high grain yield. Non-significant accessions x location interactions in the population 1, 2, 3 and 5 meant consistency of genotypic yield performance over the two locations.

It is important to note that variation in grain yield performance of accessions was non significant between the short height stratum and the tall height stratum (see Table 4.1). This outcome permited unconfounded comparisons of the effectiveness of the different selection criteria in the indirect selection for grain yield performance in the two plant height strata and negated the need to present the comparison of means between the two plant height strata.

Pertinent comparisons of means for components which showed statistical significance in the ANOVA of grain yield (Table 4.1), are presented in Tables 4.2 to 4.4. Grain yield was higher at the cooler site ART than at RA in populations 2 and 4 only (Table 4.2). Differences in performance between the parents and the mean of accessions would indicate the presence of heterosis in a given population. Such differences were only recorded in population 4 over the two locations and in population 6 at RA only. In both cases the mid- parental grain yield mean was greater than the grain yield mean of accessions, suggesting negative heterosis (Table 4.3).

The different criteria of selection are compared in Table 4.4. Accessions selected on the basis of high single- ear progeny biomass or earmass (EM), gave higher grain yields than those selected on the basis of low single-ear progeny biomass or earmass, in P_1 ($P<0.01$), P_2 ($P<0.05$), P_3 ($P<0.001$) and P_5 ($P<0.05$) over the two locations and in population 4 ($P<0.05$) at the cooler location (ART) only.

Grain yield of accessions selected on the basis of high single-ear progeny HI was also greater than that of accessions selected on the basis of low single-ear progeny HI, but in the tall height stratum of population 1 ($P<0.05$), population 3 ($P<0.01$) and population 6 ($P<0.05$) only (Table4.1).

insert page 72 with tables 4.2

4.1.2 Entry-mean heritability estimates and genetic coefficients of variability for grain yield

Entry-mean heritability estimates and genetic coefficients of variability (G.C.V.) for the grain yield are presented in Table 4.5 below, for the different plant height strata of each population. The range of entry-mean heritability estimates for grain yield were low to medium in magnitude, being 0,27 to 0,80 in the unstratified populations, 0,37 to 0,74 in the short height stratum, and 0,18 to 0,85 in the tall height stratum. Entry-mean heritability estimates averaged over the six populations in the different plant height classes were; 0,49 in the unstratified populations, 0,56 in the short height stratum and 0,40 in the tall height stratum. The magnitudes of the G.C.Vs followed a similar pattern to that of the corresponding heritability estimates of the respective populations. The ranges of the G.C.Vs in the different plant height classes were; 1,8% to 4,9% over the unstratified populations, 2,6% to 4,5% in the short height stratum and 1,0% to 5,3% in the tall height stratum. The respective means of G.C.Vs over the six populations in the different plant height classes were; 3,0% in the unstratified populations, 3,5% in the short height stratum and 2,6% in the tall height stratum.

Standard errors of the heritability estimates for grain yield in Table 4.5 were rather high because these, according to Knapp *et al.* (1985), are only approximations which are subject to high sampling variation. Further more the lack of robustness of this statistic is due to the use of squared terms in the form of genotypic and phenotypic variances, in estimating H^2 (Dikerson, 1969) and the assumption of normality or symmetry of the distribution of the H^2 estimate, which is often not met (Knapp *et al.,*1985).

Table 4.5: Entry-mean heritability estimates (H^2), standard errors (S.E.) and exact 90% confidence limits of those heritability estimates, and genetic coefficients of variability for grain yield (kg/ha) measured in six wheat populations grown at two locations in winter 1994

Height stratum and population	Entry-mean H^2	S.E. of H^2	Exact 90% CL of H^2		Genetic coefficient of variability (%)
			Upper	Lower	
Unstratified					
P_1	0,80	0,256	0,89	0,64	4,9
P_2	0,64	0,262	0,80	0,33	3,5
P_3	0,50	0,269	0,73	0,07	3,4
P_4	0,39	0,277	0,67	-0,13	2,3
P_5	0,27	0,286	0,61	-0,35	1,8
P_6	0,33	0,281	0,64	-0,25	2,0
Short height stratum					
P_1	0,74	0,359	0,90	0,37	4,5
P_2	0,64	0,365	0,86	0,11	3,9
P_3	0,57	0,369	0,83	-0,06	4,2
P_4	0,37	0,387	0,75	-0,55	3,0
P_5	0,57	0,369	0,83	-0,06	2,8
P_6	0,44	0,380	0,78	-0,38	2,6
Tall height stratum					
P_1	0,85	0,356	0,94	0,63	5,3
P_2	0,71	0,361	0,88	0,28	3,3
P_3	0,23	0,402	0,69	-0,90	2,0
P_4	0,18	0,408	0,67	-1,03	1,0
P_5	0,24	0,401	0,69	-0,88	2,3
P_6	0,18	0,409	0,67	-1,03	1,4

4.2 Results of Experiment 2: Single-ear progenies data

Analysis of variance and tables of means are presented for the different single-ear progeny attributes, biomass, earmass, harvest index and plant height. These will be described separately below for each attribute.

4.2.1 Biomass yield of single- ear progenies

Analysis of variance of biomass yield (biomass) of single- ear progenies is presented in Table 4.6. Significant ($P<0.001$) genotype x location interaction was observed in the expression of single-ear progeny biomass in all the six populations.Singnificant differences ($P<0.001$) in the expression of single-ear progeny biomass were also noted between accessions selected on the basis of high biomass or earmass and those selected on the basis of low biomass or earmass in the short height stratum of all the six populations, and in the tall height stratum of population 1 ($P<0.001$), and populations 2,3 and 5 ($P<0.01$).

Means of single-ear progeny biomass are presented in Tables 4.7 and 4.8. Greater mean ($P<0.001$) single-ear progeny biomass was obtained for accessions in the tall height stratum than in the short height stratum of populations 1 to 5, being similar in both plant height strata population 6 (Table 4.7). In Tables 4.6 and 4.8, it is shown that accessions selected on the basis of high single-ear progeny biomass or earmass gave significantly higher ($P<0.001$) biomass than those selected on the basis of low biomass or earmass in the short height stratum of all the six populations and in the tall height stratum of populations 1 ($P<0.001$), 2,3 and 5 ($P<0.01$). It was only in population 4 in the tall stratum, that similar single-ear progeny biomass were obtained for the high biomass or earmass and low biomass or earmass selection groups. Moreover in this population 4, the low HI selection group gave higher ($P<0.01$) single-ear progeny biomass than the high HI selection group in the tall height stratum and vice versa in the short height stratum (Table 4.8).

Insert 3 table4.7 and 4.8

Estimates of entry-mean heritabilities and G.C.Vs for single-ear progeny biomass measured in the different plant height strata of the six populations are presented in Table 4.9. Entry-mean heritability estimates (0,84 to 0,92) were high in the unstratified populations and also in the short height stratum (0,86 to 0,89). In the tall height stratum however, heritability estimates (0,44 to 0,95) were intermediate to high. Means of entry-mean heritability estimates over the six populations were 0,89 in the unstratified population, 0,87 in the short height stratum and 0,77 in the tall height stratum. Genetic coefficients of variability (3,5% to 5,6%) were correspondingly high in the unstratified populations and in the short height stratum (3,4% to 4,5%) of the populations. In the tall height stratum, low G.C.Vs (1,4% to 3,3%) were obtained in populations 2, 3, 4 and 5 but were uniquely high in population 1 (5,0%) and in population 6 (4,5 %).

Means of genetic coefficients of variability in the different plant height classes for single-ear progeny biomass were; 4,4% in the unstratified populations, 4,0% in the short height stratum and 3,2% in the tall height stratum. Thus higher genotypic variability for single ear progeny biomass was encountered in the unstratified and the short height strata of the populations than in the tall height stratum, for most of the populations.

Table 4.9: Entry mean heritability estimates (H^2), standard errors (S.E.) and exact 90% confidence limits of those heritability estimates and genetic coefficients of variability for single-ear progeny biomass (g/0,9m^2) measured in six wheat populations grown at three locations in winter 1994

Height stratum and population	Entry-mean H^2	S.E. of H^2	Exact 90% CL of H^2		Genetic coefficient of variability (%)
			Upper	Lower	
Unstratified					
P_1	0,89	0,254	0,93	0,82	5,6
P_2	0,89	0,254	0,93	0,82	4,5
P_3	0,92	0,254	0,95	0,86	5,1
P_4	0,88	0,254	0,92	0,80	3,5
P_5	0,84	0,255	0,90	0,74	3,6
P_6	0,92	0,254	0,95	0,87	4,2
Short height stratum					
P_1	0,87	0,354	0,94	0,74	4,5
P_2	0,86	0,354	0,93	0,72	3,4
P_3	0,88	0,354	0,94	0,76	4,6
P_4	0,89	0,354	0,95	0,77	3,6
P_5	0,87	0,354	0,94	0,74	4,1
P_6	0,87	0,354	0,94	0,77	4,0
Tall height stratum					
P_1	0,85	0,355	0,93	0,70	5,0
P_2	0,78	0,356	0,89	0,55	2,6
P_3	0,83	0,355	0,92	0,66	3,2
P_4	0,76	0,356	0,88	0,52	2,3
P_5	0,44	0,368	0,73	-0,14	1,4
P_6	0,95	0,354	0,98	0,90	4,5

4.2.2 Earmass of single-ear progenies

The analyses of variance of single-ear progeny earmass are presented in Table 4.10 below for the different populations. The magnitude of single-ear progeny earmass varied across sites. Highly significant differences ($P<0.001$) in single-ear progeny earmass were observed among the wheat genotypes (accessions and parents) in all the six populations. Significant differences ($P<0.001$) in the magnitude of single-ear progeny earmass were observed between the two plant height strata

Insert 4 table 4.10

in populations 1,2,3 and 5, and between the high biomass or earmass and low biomass or earmass selection groups in the short height stratum of populations 2,3,4,5 and 6 ($P<0.001$) and the tall height stratum of populations 1($P<0.01$), 2 and 5 ($P<0.001$).

Means of single-ear progeny earmass are presented in Tables 4.11 and 4.12. Responses to earmass selection were similar to those reported to biomass selection. Earmass of single- ear progenies was significantly greater ($P<0.001$) in the tall height stratum than in the short height stratum of populations 1,2,3 and 5, but similar in the two plant height strata in populations 4 and 6. Accessions selected on the basis of high biomass or earmass gave significantly greater ($P<0.001$) single-ear progeny earmass than those selected on the basis of low biomass or earmass in the short height stratum of populations 2,3,4,5 and 6 and in populations 1 ($P<0.01$), 2 and 5 ($P<0.001$) (Table 4.12), despite the presence of significant genotype × location interaction (Table 4.10). Interactions of these contrasts with location were not confounding since they were generally due to differences in magnitude rather than due to crossovers in genotypic performance over locations.

It is shown in Table 4.13 that entry-mean heritability estimates (0,75 to 0,91 with mean 0,87 in the unstratified; 0,74 to 0,91 with mean 0,85 in the short height stratum and 0,73 to 0,90 with mean 0,84 in the tall height stratum) were high. G.C.Vs of single-ear progeny earmass was somewhat higher in the unstratified populations (4,7% to 7,3%) and in the short height stratum (4,2% to 5,7%) than in the tall height stratum (3,2% to 7,4%). Means of G.C.Vs over populations were 5,7% in the unstratified populations, 5,5% in the short height stratum and 4,8% in the tall height stratum.

Insert table 4.11 and 4.12

Table 4.13: Entry mean heritability estimates (H^2), standard errors (S.E.) and exact 90% confidence limits of those heritability estimates and genetic coefficients of variability for single-ear

progeny earmass (g/0,9m^2) measured in six wheat populations grown at three locations in winter 1994

Height stratum and population	Entry-mean H^2	S.E. of H^2	Exact 90% CL of H^2		Genetic coefficient of variability (%)
			Upper	Lower	
Unstratified					
P_1	0,75	0,256	0,85	0,59	4,7
P_2	0,88	0,254	0,93	0,80	6,6
P_3	0,89	0,254	0,93	0,81	5,4
P_4	0,87	0,255	0,92	0,79	4,9
P_5	0,89	0,254	0,93	0,82	5,0
P_6	0,91	0,254	0,94	0,85	7,3
Short height stratum					
P_1	0,82	0,355	0,91	0,64	4,7
P_2	0,85	0,355	0,93	0,70	5,5
P_3	0,74	0,357	0,87	0,47	4,2
P_4	0,89	0,354	0,95	0,77	5,4
P_5	0,89	0,354	0,95	0,77	5,7
P_6	0,91	0,354	0,96	0,82	7,4
Tall height stratum					
P_1	0,73	0,357	0,87	0,44	4,2
P_2	0,88	0,354	0,94	0,75	6,2
P_3	0,85	0,355	0,93	0,69	3,2
P_4	0,87	0,354	0,94	0,74	4,6
P_5	0,83	0,355	0,92	0,65	3,3
P_6	0,90	0,354	0,95	0,80	7,4

4.2.3 Harvest index of single-ear progenies

Analyses of variance of HI of single-ear progenies are presented in Table 4.14. Significant ($P<0.001$) genotype × location interaction in the expression of this single-ear progeny trait was observed in all the six populations (Table 4.14). Populations 1, 4 and 5 showed differences in HI of single-ear progenies between accessions in the two plant height strata, but these differences were associated with significant interaction with location (Table 4.14).

Insert table 4.14 execl

Means of single-ear progeny HI are presented in Tables 4.15 and 4.16. In populations 1 and 2 single-ear progeny HI was greater ($P<0.05$) in the short height stratum than in the tall height stratum in at least two of the three locations. The reverse was observed in populations 1 and 5 at ORIBI. Significantly higher HI means were obtained in the accessions which were selected on the basis of high HI of single-ear progenies when compared to that obtained in the accessions selected on the basis of low HI of single-ear progenies in both the short and tall height strata in populations 1, 2, 3 and 6. For populations 4 and 5, the positive response to HI index selection was only noted in the tall height stratum (Table 4.16).

Entry-mean heritability estimates and genetic coeffients of variability for single-ear progeny HI are presented in Table 4.17. These estimates were generally lower than those obtained for single-ear progeny biomass and earmass, and those for grain yield. The ranges of entry-mean heritability estimates were; 0,38 to 0,71 in the unstratified populations, 0,09 to 0,75 in the short height stratum and 0,16 to 0,74 in the tall height stratum. Means of entry-mean heritability estimates over the six populations were; 0,53 in the unstratified populations, 0,48 in the short height stratum and 0,58 in the tall height stratum. Ranges and means of G.C.Vs in the different plant height classes were 1,6% to 3,7% and mean 2,6% in the unstratified populations, 0,7% to 3,9% and mean 2,3% in the short height stratum and 1,0% to 3,5% and mean 2,7% in the tall height stratum.

Insert 4.15 and 4.16

Table 4.17: Entry mean heritability estimates (H^2), standard errors (S.E.) and exact 90% confidence limits of those heritability estimates and genetic coefficients of variability for single-ear progeny HI (%) measured in six wheat populations grown at three locations in winter 1994

Height stratum and population	Entry - mean H^2	S.E. of H^2	Exact 90% CL of H^2		Genetic coefficient of variability (%)
			Upper	Lower	
Unstratified					
P_1	0,32	0,269	0,59	-0,11	1,8
P_2	0,61	0,259	0,76	0,37	3,1
P_3	0,49	0,262	0,69	0,16	2,3
P_4	0,69	0,257	0,81	0,49	2,8
P_5	0,38	0,266	0,62	-0,02	1,6
P_6	0,71	0,257	0,82	0,52	3,7
Short height stratum					
P_1	0,75	0,357	0,87	0,48	3,1
P_2	0,53	0,364	0,77	0,04	2,5
P_3	0,14	0,387	0,58	-0,76	1,2
P_4	0,64	0,359	0,83	0,27	2,2
P_5	0,09	0,390	0,56	-0,85	0,7
P_6	0,74	0,357	0,87	0,47	3,9
Tall height stratum					
P_1	0,16	0,386	0,59	-0,72	1,0
P_2	0,67	0,359	0,84	0,33	3,7
P_3	0,74	0,357	0,87	0,48	3,1
P_4	0,61	0,361	0,81	0,20	2,5
P_5	0,65	0,359	0,83	0,28	2,4
P_6	0,67	0,359	0,84	-0,33	3,5

4.2.4 Plant height of single-ear progenies

Analyses of variance of plant height of single-ear progenies are presented in Table 4.18.

As expected, large and significant differences ($P<0.001$) in plant height were observed between the two plant height strata.

Insert 4.18 and 4.19

Plant height variation within both the short stratum and the tall height stratum was relatively smaller than the between height strata variation, though significant in populations 1 ($P<0.05$ in both strata) , 2 and 4 ($P<0.01$ in the tall height stratum), 5 ($P<0.5$ in the tall height stratum) and 6 ($P<0.01$ in the short height stratum) (Table 4.18). Comparisons of mean plant stature of accessions in the different plant height strata are presented in Table 4.19: Accessions selected on the basis of short stature were consistently shorter statured than those selected on the basis of tallness (Table 4.19 above).

Estimates of entry-mean heritabilities of plant height (cm) of single-ear progenies are presented in Table 4.20. These estimates were higher (0,82 to 0,91) in the unstratified populations than in the short and tall plant height strata (0,12 to 0,65). Genetic coefficient of variability of plant height followed a similar pattern, ranging between 2,6% and 4,2% in the unstratified population and between 0,6% and 2,6% in the short height and tall height strata (Table 4.20).

Table 4.20: Entry mean heritability estimates (H^2), standard errors (S.E.) and exact 90% confidence limits of those heritability estimates and genetic coefficients of variability for single-ear progeny plant height (cm) measured in six wheat populations grown at three locations in winter 1994

Height stratum and population	Entry-mean H^2	S.E. of H^2	Exact 90% CL of H^2		Genetic coefficient of variability (%)
			Upper	Lower	
Unstratified					
P_1	0,89	0,254	0,93	0,82	4,2
P_2	0,88	0,254	0,93	0,80	4,1
P_3	0,82	0,255	0,89	0,70	4,0
P_4	0,91	0,254	0,95	0,85	3,4
P_5	0,86	0,255	0,91	0,77	3,5
P_6	0,82	0,255	0,89	0,71	2,6
Short height stratum					
P_1	0,60	0,361	0,80	0,18	2,2
P_2	0,28	0,377	0,65	-0,48	1,1
P_3	0,12	0,388	0,57	-0,80	0,7
P_4	0,55	0,363	0,78	0,07	1,7
P_5	0,13	0,388	0,57	-0,79	0,6
P_6	0,51	0,365	0,76	-0,01	2,6
Tall height stratum					
P_1	0,60	0,361	0,80	0,18	1,6
P_2	0,61	0,361	0,81	0,20	2,1
P_3	0,68	0,358	0,84	0,34	1,6
P_4	0,61	0,361	0,81	0,21	1,8
P_5	0,52	0,364	0,76	0,02	1,4
P_6	0,36	0,372	0,69	-0,30	1,1

4.3 Associations between grain yield performance of wheat accessions and their respective single-ear progeny plot attributes.

Phenotypic correlation coefficients between mean grain yields measured in replicated large plot trials and single ear progeny plot attributes, biomass, earmass and HI, measured in the previous season as presented in Appendix Tables 3.1 to 3.6 are reported below for the different criteria of selection.

4.3.1 Correlations between grain yield in large plot trials and single-ear progeny plot biomass

Phenotypic and genotypic correlation coefficients between grain yield and single-ear progeny plot biomass are presented in Table 4.21. Phenotypic correlation 0,40 ($P<0.05$) to 0,53 ($P<0.01$) between grain yield and single-ear progeny plot biomass were moderate in all the unstratified populations. They were high (0,65 to 0,74; $P<0.01$) in populations 1, 3 and 4 and moderate but non significant (0,44 to 0,49) in populations 2, 5 and 6, in the short height stratum. It was only population 6 which gave high phenotypic correlation (0,63; $P<0.01$) in the tall height stratum. The remaining populations gave low to moderate non significant phenotypic correlations (0,01 to 0,49) between grain yield and single-ear progeny plot biomass in this tall height stratum.

Genotypic correlation coefficients (0,60 to 0,99) were moderate to high in all the six populations in both the unstratified group and short height stratum. They were low to moderate (0,03 to 0,64) in the tall height stratum of populations 1, 2, 3 and 4 but very high (0,99) in populations 5 and 6. High genotypic correlation coefficients arose from high values of the phenotypic correlation coefficients and for very low values of the heritability estimates of the auxiliary and / or the responding trait(s) since rg was calculated as the ratio of the phenotypic correlation coefficient to the geometric mean of the two heritabilities (see Section 3.2.4). Sampling errors in the estimation of heritabilities and standard errors of the responding and auxiliary traits gave some estimates of genotypic correlation coefficients which were greater than unity, which, according to Bos (1981), are not unusual. Such values were in this study, adjusted to the realistic genotypic coefficient value of 0.99.

Table 4.21: Phenotypic correlation coefficients (rp) and genotypic correlation coefficients

(rg) between mean grain yield in 1994 large plot trials and single-ear progeny plot biomass measured in the previous year for 30 accessions in the intact populations and in 15 accessions in either the short height stratum or the tall height stratum of each of the six wheat populations (P)

Plant height stratum and population	rp	rg	S.E. of rg
Unstratified			
P_1	0,51 **	0,60	± 0,192
P_2	0,48 **	0,64	± 0,204
P_3	0,46 **	0,68	± 0,208
P_4	0,40 *	0,69	±0,241
P_5	0,45 *	0,94	± 0,065
P_6	0,53 **	0,97	± 0,030
Short height stratum			
P_1	0,71 **	0,88	± 0,099
P_2	0,49 ns	0,66	± 0,273
P_3	0,74 **	0,99	± 0,024
P_4	0,65 **	0,99	± 0,030
P_5	0,48 ns	0,68	± 0,276
P_6	0,44 ns	0,70	± 0,297
Tall height stratum			
P_1	0,35 ns	0,41	± 0,347
P_2	0,49 ns	0,66	± 0,273
P_3	0,26 ns	0,59	± 0,559
P_4	0,01 ns	0,03	± 0,038
P_5	0,47 ns	0,99	± 0,025
P_6	0,63 **	0,99	± 0,043

*, ** = statistically significant at the 5% and 1% probability levels, respectively,
ns = not significant at 5% level of probability.

4.3.2 Correlation between grain yield in large plot trials and single-ear progeny plot earmass

Phenotypic and genotypic correlation coefficients between mean grain yields of accessions in trials and their respective single-ear progeny plot earmass measured in the previous season, are presented in Table 4.22 .

Table 4.22: Phenotypic correlation coefficients (rp) and genotypic correlation coefficients

(rg) between mean grain yield in 1994 large plot trials and single-ear progeny plot earmass measured in the previous year for 30 accessions in the intact population and in 15 accessions in either the short height stratum or the tall height stratum of each of the six wheat populations (P)

Plant height stratum and population	rp	rg	S.E. of rg
Unstratified			
P_1	0,57 **	0,73	± 0,192
P_2	0,48 **	0,64	± 0,204
P_3	0,46 **	0,68	± 0,208
P_4	0,40 *	0,69	± 0,241
P_5	0,45 *	0,94	± 0,065
P_6	0,48 **	0,88	± 0,107
Short height stratum			
P_1	0,83 ***	1,06	± 0,021
P_2	0,79 ***	1,07	± 0,023
P_3	0,91 ***	1,40	± 0,022
P_4	0,70 ***	1,22	± 0,030
P_5	0,71 ***	0,99	± 0,005
P_6	0,42	0,66	± 0,325
Tall height stratum			
P_1	0,40 ns	0,51	± 0,336
P_2	0,76 **	0,96	± 0,033
P_3	0,53 *	1,19	± 0,041
P_4	0,01 ns	0,03	± 0,951
P_5	0,61 *	1,37	± 0,035
P_6	0,55 *	1,36	± 0,042

*, **, *** = statistically significant at the 5%, 1% and 0,1% probability levels, respectively,
ns = not significant at 5% level of probability.

In the intact or unstratified population, phenotypic correlation coeffients between grain yield and single-ear progeny plot earmass ranged between 0,40 ($P<0.05$) to 0,57 ($P<0.01$). The corresponding genotypic correlation coeffients (0,64 to 0,94) were moderate to high. Of the three single-ear progeny plot attributes, earmass of single-ear progenies gave the highest phenotypic correlation coeffients (0,71; $P<0.05$ to 0,91; $P<0.01$) in five out of the six populations, in the short height stratum.

Apart from the rather weak relationship in population 6 (rp = 0.42; rg = 0.66) the genotypic

correlation coeffients between grain yield and single-ear progeny earmass, in the short height stratum, were very high (≥0,99) in the other five populations. Phenotypic correlation coefficients were moderate in the tall height stratum of populations 2, 3, 5 and 6 (0,53; P<0.05 to 0,76; P<0.01), and were associated with high genotypic correlation coefficients which ranged between 0,96 to 0,99. Relationships in the tall height stratum of population 1 (rp = 0,40; rg = 0,51) and population 4 (rp =0,01; rg = 0,03) were rather weak and nonsignificant.

4.3.3 Correlation between grain yield in large plot trials and single-ear progeny plot harvest index

Phenotypic and genotypic correlation coefficients between grain yield and harvest index of single-ear progenies are presented in Table 4.23. The relationship between grain yield in trials and single-ear progeny harvest index was generally weak with the exception of that of population 2, which gave moderate but significant positive phenotypic correlation coeffients (0,63; P<0.001) in the unstratified population, 0,66 (P<0.01) in the short height stratum and 0,56 (P<0.05) in the tall height stratum. Populations 3 and 5 also gave moderate correlation coeffients (0,46; ns to 0,52; P<0.05) between the two attributes. It was only in these three populations in which the genotypic correlation coeffients between grain yield and HI were appreciably high (0,71 to 0,99).

Table 4.23: Phenotypic correlation coefficients (rp) and genotypic correlation coefficients (rg) between mean grain yields in 1994 large plot trials and single ear progeny plot harvest index measured in the previous year for 30 accessions in the unstratified population and in 15 accessions in either the short height stratum or the tall height stratum of each of the six wheat populations (P)

Plant height stratum and population	rp	rg	S.E. of rg
Unstratified			
P_1	0,23 ns	0,45	± 0,410
P_2	0,63 ***	0,99	± 0,019
P_3	0,49 **	0,99	± 0,011
P_4	0,05 ns	0,09	± 0,512
P_5	0,38 *	0,99	± 0,023
P_6	0,03 ns	0,06	± 0,558
Short height stratum			
P_1	0,26 ns	0,35	± 0,422
P_2	0,66 **	0,99	± 0,018
P_3	0,52 *	0,99	± 0,010
P_4	0,19 ns	0,39	± 0,646
P_5	0,46 ns	0,99	± 0,008
P_6	0,07 ns	0,12	± 0,633
Tall height stratum			
P_1	0,23 ns	0,63	± 0,611
P_2	0,56 *	0,81	± 0,179
P_3	0,46 ns	0,99	± 0,004
P_4	0,01 ns	0,03	± 1,151
P_5	0,28 ns	0,71	± 0,478
P_6	0,01 ns	0,03	± 1,099

*, **, *** = statistically significant at the 5%, 1% and 0,1% probability levels, respectively,
ns = statistically significant at 5% level of probability.

4.4 Interrelationships of single-ear progeny plot traits

Phenotypic and genotypic correlations between the single-ear progeny plot traits, biomass, earmass, harvest index and plant height were estimated to ascertain the degree of correlated responses in the other attributes when any one of them is under selection. These relationships are reported separately below for the different plant height strata.

4.4.1 Interrelationships of biomass, earmass, harvest index and plant height of single-ear progeny plots in the unstratified populations.

Phenotypic and genotypic correlations among single-ear progeny traits in the unstratified populations are presented in Table 4.24. Low to moderate significant phenotypic and genotypic correlation coefficients were obtained between plant height and biomass (rp = 0,23; P<0.05 to 0,57; P<0.001), (rg = 0,44; P<0.001 to 0,89; P<0.001) and between plant height and earmass (rp = 0,37; P<0.001 to 0,81; P<0.001) (rg = 0,38; P<0.001 to 0,99; P<0.001). Harvest index was consistently positively correlated with earmass (rp = 0,24; P<0.05 to 0,76; P<0.001), (rg = 0,30 to 0,80; P<0.001) but tended to be negatively correlated with biomass (rp = -0,58; P<0.001 to 0,24); P<0.05, (rg = -0,56; P<0.001 to 0,28; P<0.05). Relationship between harvest index and plant height was inconsistent across populations. Plant height was positively correlated with HI in populations 5 and 6 (rp = 0,20 to 0,34; P<0.01)(rg =0,53; P<0.01 to 0,86; P<0.001) and negatively correlated with HI in population 1 (rp = -0,22; P<0.05, rg = -0,99; P<0.001), while it was weak in population 2,3 and 4 (rp = 0,02 ; ns to 0,24; P<0.05) (rg =0,01; ns to 0,29; ns).

4.4.2 Interrelationships of biomass, earmass, harvest index and plant height of single-ear

progeny plots in the short height stratum of six wheat populations.

Phenotypic and genotypic correlations among the above single-ear progeny traits are presented in Table 4.25. Plant height was significantly correlated with biomass (rp = 0,23 to 0,61; P<0.001) (rg = 0,39; P<0.01 to 0,96; P<0.001). Biomass was strongly correlated with earmass (rp = 0,38; P<0.01 to 0,83; P<0.001) (rg = 0,40; P<0.01 to 0,98; P<0.001). As was the case in the unstratified populatuions, harvest index was positively correlated with earmass (rp = 0,24 to 0,81; P<0.001) (rg = 0,34; P<0.05 to 0,96; P<0.001). Biomass and harvest index tended to be negatively correlated (rp = -0,22 to -0,59; P<0.001) (rg = -0,06 to –0,59; P<0.001) in populations 1, 2, 3and 5 but these were positively correlated in population 4 and 6 (rp = 0,33; P<0.05 to 0,37; P<0.05) (rg = 0,31; P<0.05 to 0,41; P<0.01).

Correlations between plant height and harvest index were weak and also tended to be negative in the short height strata. They were however positive and significant in populations 4 and 6 (rp = 0,39; P<0.01 to 0,42; P<0.01)(rg = 0,39; P<0.01 to 0,48; P<0.01), and non significant and positive in population 5.

Table 4.24: Phenotypic (rp) and genotypic (rg) correlation coefficients for single-ear progeny attributes, biomass, earmass, harvest index and plant height measured in six unstratified wheat populations (P) grown at three locations in winter 1994

Single ear progeny attribute	Population		Single-ear progeny attribute		
			Plant height	Biomass	Earmass
Biomass	P_1	rp	0,53***		
		rg	0,74***		
	P_2	rp	0,55***		
		rg	0,89***		
	P_3	rp	0,46***		
		rg	0,88***		
	P_4	rp	0,57***		
		rg	0,63***		
	P_5	rp	0,22*		
		rg	0,44***		
	P_6	rp	0,23*		
		rg	0,38***		
Earmass	P_1	rp	0,33**	0,37***	
		rg	0,31**	0,38***	
	P_2	rp	0,57***	0,49***	
		rg	0,75***	0,90***	
	P_3	rp	0,45***	0,52***	
		rg	0,85***	0,88***	
	P_4	rp	0,53***	0,75***	
		rg	0,43***	0,99***	
	P_5	rp	0,43***	0,54***	
		rg	0,62***	0,95***	
	P_6	rp	0,36***	0,81***	
		rg	0,50***	0,94***	
Harvest index	P_1	rp	-0,22*	-0,28*	0,24*
		rg	-0,99***	-0,47***	0,30*
	P_2	rp	0,07 ns	-0,42***	0,58***
		rg	0,29**	-0,05 ns	0,80***
	P_3	rp	-0,07 ns	-0,56***	0,42***
		rg	0,01 ns	-0,17 ns	0,31**
	P_4	rp	0,24*	0,12 ns	0,75***
		rg	0,07 ns	0,48***	0,78***
	P_5	rp	0,20*	-0,58***	0,37***
		rg	0,86***	-0,32**	0,80***
	P_6	rp	0,34***	0,24*	0,76***
		rg	0,53***	0,28*	0,90***

*, **, *** = statistically significant at the 5%, 1% and 0,1% probability level respectively,
ns = not significant at 5% level of probability.
NB: $df_{(rp, rg)} = 88$.

Table 4.25: Phenotypic (rp) and genotypic (rg) correlation coefficients for single-ear progeny attributes, biomass, earmass, harvest index and plant in the short height stratum of six wheat (p) populations grown at three locations in winter 1994

Single-ear progeny attribute	Population		Single-ear progeny attribute		
			Plant height	Biomass	Earmass
Biomass	P_1	rp	0,34*		

		rg	0,39**		
	P_2	rp	0,54***		
		rg	0,96***		
	P_3	rp	0,61***		
		rg	0,89***		
	P_4	rp	0,59***		
		rg	0,65***		
	P_5	rp	0,23ns		
		rg	0,47***		
	P_6	rp	0,31*		
		rg	0,42**		
Earmass	P_1	rp	0,42**	0,38**	
		rg	0,43**	0,40**	
	P_2	rp	0,53***	0,43**	
		rg	0,73***	0,88***	
	P_3	rp	0,28ns	0,41**	
		rg	0,33*	0,85***	
	P_4	rp	0,61***	0,81***	
		rg	0,68***	0,97***	
	P_5	rp	0,40**	0,55***	
		rg	0,45**	0,93***	
	P_6	rp	0,42**	0,83***	
		rg	0,51***	0,98***	
Harvest index	P_1	rp	-0,20ns	-0,22ns	0,24ns
		rg	-0,26ns	-0,06ns	0,34*
	P_2	rp	0,05ns	-0,46**	0,60***
		rg	0,11ns	-0,38**	0,78***
	P_3	rp	-0,34*	-0,59***	0,49***
		rg	-0,21ns	-0,41**	0,52***
	P_4	rp	0,42**	0,37*	0,81***
		rg	0,39**	0,41**	0,86***
	P_5	rp	0,18ns	-0,55***	0,38**
		rg	0,25ns	-0,35*	0,79***
	P_6	rp	0,39**	0,33*	0,80***
		rg	0,48***	0,31*	0,96***

*, **, *** = statistically significant at the 5%, 1% and 0,1% probability levels, respectively,
ns = not significant at 5% probability level.
NB: $df_{(rp, rg)} = 43$.

4.4.3 Interrelationships of biomass, earmass, harvest index and plant height of single-ear progeny plots in the tall height stratum of the populations

Table 4.26 shows the phenotypic and genotypic correlations among biomass, earmass, harvest index and plant height. Plant height and biomass were generally weakly correlated in the tall height stratum except for populations 1 and 4 in which positive significant correlations were obtained (rp = 0,34; P<0.05 to 0,48; P<0.001) (rg = 0,39; P<0.05 to 0,50; P<0.001). Plant height and earmass were moderately positively correlated in populations 2, 4, 5 and 6 (rp = 0,35; P<0.05 to 0,46; P<0.01) (rg = 0,37; P<0.05 to 0,48; P<0.001), but not in populations 1 and 3. Correlation coefficients between biomass and earmass were significant and positive in the tall height stratum (0,21 to 0,80; P<0.001) (rg = 0,36; P<0.05 to 0,97; P<0.001), but these were not as strong as those encountered in the unstratified population and in the short height stratum. Plant height and harvest index were weakly correlated in the tall height stratum in the five populations but were strongly positively correlated in population 6 (rp = 0,42; P<0.01; rg = 0,51; 0.001). Biomass and harvest index were generally negatively correlated in the tall height stratum (rp = 0,17 to –0,77; P<0.01 rg = 0,22 to –0,46; P<0.01). Earmass and harvest index were as in other plant height strata strongly positively correlated in this tall height stratum of the populations (rp = 0,35; P<0.05 to 0,73; P<0.001) (rg = 0,38; P<0.01 to 0,92; P<0.001).

Table 4.26: Phenotypic (rp) and genotypic (rg) correlation coefficients for single-ear progeny attributes, biomass, earmass, harvest index and plant height in the tall height stratum of six wheat populations (P) grown at at three locations in winter 1994

Single-ear progeny attribute	Population		Single-ear progeny attribute		
			Plant height	Biomass	Earmass
Biomass	P_1	rp	0,34*		
		rg	0,39**		
	P_2	rp	0,13ns		
		rg	0,21ns		
	P_3	rp	-0,19ns		
		rg	-0,13ns		
	P_4	rp	0,48***		
		rg	0,50***		
	P_5	rp	0,04ns		
		rg	0,06ns		
	P_6	rp	0,14ns		
		rg	0,19ns		
Earmass	P_1	rp	0,01ns	0,21	
		rg	0,11ns	0,36*	
	P_2	rp	0,37*	0,32*	
		rg	0,42**	0,63***	
	P_3	rp	-0.02ns	0,23ns	
		rg	0,26ns	0,42**	
	P_4	rp	0,46**	0,71***	
		rg	0,48***	0,86***	
	P_5	rp	0,35*	0,37**	
		rg	0,42**	0,75***	
	P_6	rp	0,35*	0,80***	
		rg	0,37*	0,97***	
Harvest index	P_1	rp	-0,14ns	-0,29*	0,35*
		rg	-0,22ns	-0,49***	0,38**
	P_2	rp	0,23ns	-0,46**	0,69***
		rg	0,24ns	-0,23ns	0,78***
	P_3	rp	0,13ns	-0,77***	0,45**
		rg	0,19ns	-0,28ns	0,48***
	P_4	rp	0,19ns	0,04ns	0,73***
		rg	0,16ns	0,09ns	0,84***
	P_5	rp	0,25ns	-0,69***	0,41***
		rg	0,36*	-0,38***	0,69***
	P_6	rp	0,42**	0,17ns	0,72***
		rg	0,51***	0,22ns	0,92***

*, **, *** = statistically significant at the 5%, 1% and 0,1% probability levels, respectively,
ns = not significant at 5% probability level.
NB: $df_{(rp, rg)} = 43$.

4.5 Relative Selection Efficiencies (RSE) of indirectly selecting for high grain yield using biomass, earmass or harvest index of single-ear progenies as auxiliary traits

The relative selection efficiencies of indirectly selecting for high grain yield performance in wheat grown under irrigation, as a result of selecting high phenotypic expressions of either biomass, earmass or harvest index of single-ear progeny plots in different plant height strata, are shown in tables 4.27 to 4.29. RSE values greater than unity were obtained in cases where the heritability estimate for the responding trait grain yield was much smaller than the estimate of the phenotypic correlation coeffient between itself and the auxiliary trait. Some of the RSE values were associated with large standard errors because such estimation of RSE involves the ratio h_x/h_y, which can differ markedly for small differences in the heritability estimates (Searle, 1965).

4.5.1 Relative Selection Efficiency (RSE) of indirect over direct selection for grain yield using single-ear progeny plolt biomass as the auxiliary trait

RSE values for indirectly selecting grain yield using biomass of single-ear progeny plots as the selection trait were consistently high for the unstratified populations and also for the short height stratum (0,63 to 1,74) Table 4.27). In the tall plant height stratum, however, low RSE values were obtained particularly in population 4 (0,05) and also in population 1 (0,41). The remaining four populations 2, 3, 5 and 6 gave high RSE values in the tall height stratum as well (0,69 to 3,48).

Table 4.27 Relative Selection Efficiency (RSE) of indirect over direct selection for grain yield in different plant height strata when biomass of single-ear progeny plots measured in the preceding year was used as the auxiliary trait among accessions of six wheat populations (P)

Plant height stratum and	RSE	S.E. of RSE

population		
Unstratified		
P_1	0,63	± 0,254
P_2	0,75	± 0,304
P_3	0,92	± 0,391
P_4	1,03	± 0,518
P_5	1,65	± 0,953
P_6	1,63	± 0,814
Short height stratum		
P_1	0,95	± 0,326
P_2	0,77	± 0,427
P_3	1,29	± 0,527
P_4	1,74	± 1,086
P_5	0,84	± 0,477
P_6	0,99	± 0,634
Tall height stratum		
P_1	0,41	± 0,392
P_2	0,69	± 0,393
P_3	1,11	± 1,134
P_4	0,05	± 0,862
P_5	1,95	± 1,713
P_6	3,48	± 3,811

4.5.2 Relative Selection Efficiency (RSE) of indirect over direct selection for grain yield using single-ear progeny plot earmass as the auxiliary trait

Indirect selection for grain yield using single-ear progeny earmass is compared with the direct selection for grain yield performance in Table 4.28. Relative selection efficiencies (0,71 to 2.32) of using single-ear progeny earmass in the selection for grain yield performance of irrigated wheat were very high in the short plant height stratum and also in the unstratified populations. However, population 4 with RSE value of 0,05, followed by population 1 (RSE = 0,47) did not respond to single-ear progeny earmass selection in the tall height stratum. The remaining four populations 2, 3, 5, and 6 gave very high RSE (1,07 to 3,04) values in the tall height stratum.

Table 4.28: Relative Selection Efficiency (RSE) of indirect over direct selection for grain yield in different plant height strata when earmass of single-ear progeny plots measured in the preceding year was used as the auxiliary trait among accessions of six wheat populations (P)

Plant height stratum and population	RSE	S.E. of RSE
Unstratified		
P_1	0,71	± 0,241
P_2	1,16	± 0,298
P_3	1,20	± 0,425
P_4	0,98	± 0,508
P_5	2,32	± 1,326
P_6	1,48	± 0,750
Short height stratum		
P_1	1,12	± 0,311
P_2	1,23	± 0,430
P_3	1,59	± 0,641
P_4	1,88	± 1,174
P_5	1,24	± 0,513
P_6	0,95	± 0,626
Tall height stratum		
P_1	0,47	± 0,378
P_2	1,07	± 0,344
P_3	2,26	± 2,013
P_4	0,05	± 0,862
P_5	2,53	± 2,241
P_6	3,04	± 3,266

4.5.3 Relative Selection Efficiency (RSE) of indirect over direct selection for grain yield using single-ear progeny plot harvest index as the auxiliary trait

RSE values comparing indirect selection for grain yield using single-ear progeny harvest index with direct yield evaluation , are presented in Table 4.29.The effectiveness of harvest index of single-ear progenies in the selection for grain yield performances was sporadic in all the plant height strata. Half the number of populations, i.e. P2, P3 and P5, gave high RSE values (0,79 to

1,96) in all the plant height strata but P1, P4 and P6 did not at all respond to single ear harvest index selection over all the three plant height classes.

Table 4.29: Relative Selection Efficiency (RSE) of indirect over direct selection for grain yield in different plant height strata when harvest index of single-ear progeny plots measured in the preceding year was used as the auxiliary trait among accessions of six wheat populations (P)

Plant height stratum and population	RSE	S.E. of RSE ±
Unstratified		
P_1	0,29	± 0,291
P_2	0,99	± 0,294
P_3	0,98	± 0,396
P_4	0,13	± 0,426
P_5	1,40	± 0,834
P_6	0,09	± 0,463
Short height stratum		
P_1	0,35	± 0,430
P_2	1,03	± 0,416
P_3	0,91	± 0,478
P_4	0,51	± 0,643
P_5	0,80	± 0,473
P_6	0,16	± 0,566
Tall height stratum		
P_1	0,27	± 0,396
P_2	0,79	± 0,377
P_3	1,96	± 1,750
P_4	0,05	± 0,862
P_5	1,16	± 1,146
P_6	0,06	± 0,867

4.6 Inheritance of plant height, biomass, earmass, harvest index and number of productive tillers in a spring wheat cross

4.6.1 Generation means

Generation means and their standard errors are presented in Tables 4.30 and 4.31, together with mid-parental derivations, better parental derivations and individual scaling tests, for the wheat cross Sengwa x Nata which was grown in winter 1994 at ART and ORIBI. Differences in plant stature between the two wheat varieties, Nata and Sengwa, were maintained at both locations, Nata being taller than Sengwa. Means of single plant biomass and those of single plant earmass were greater at ORIBI than at ART, across the generations. Means of reproductive tillers per plant were higher at ORIBI in the parental and BC1 generations only but were lower at this location in the F2 generation than at ART. Except for the F1 generation which showed similar HI at both locations, single plant HI was higher at ORIBI than at ART.

4.6.2 Heterosis

Expression of heterosis was similar for plant height at the two locations (Tables 4.30 and 4.31), with evidence of significant ($P<0.001$) positive mid-parent heterosis (5,1 and 3,2 cm), and negative better parent heterosis (-3,1 and –7,1cm). Significant ($P<0.001$) negative mid-parent and better-parent negative heterosis were encountered for HI at both locations. Heterotic response was different at the two locations for biomass per plant, earmass per plant and for reproductive tillers per plant. Significant ($P<0.001$) and positive mid-parent and better- parent heterosis were observed at ART but negative heterosis was noted at ORIBI, for these characters.

Insert table 4.30 and 4.31

The heterotic responses were respectively 11,8 and 11,5g/0,9m^2 for mid-parent and better-parent heterosis in biomass per plant at ART, 6,0 and 3,4 g/0,9m^2 for mid-parent and better parent heterosis in earmass per plant at ART, and 2,1 and 1,5 for mid-parent and better parent heterosis

fo number of productive tillers per plant. At ORIBI, the heterotic responses were –18,5 g/0,9m^2 and –19,8g/0,9m^2 in biomass per plant, -18,5 and –20,9 g/0,9m^2 in earmass per plant, and –1,6 and –4,3 g/0,9m^2 for number of reproductive tillers per plant , for mid-parent and better parent heterosis, respectively.

4.6.3 Individual scaling tests

Individual scaling tests are again shown in Tables 4.30 and 4.31 for the two locations. Except for biomass per plant at ART, the remaining four single plant characters showed one or more significant individual scaling tests at both locations. At ORIBI, plant height and reproductive tillers per plant showed significance in the A, C and D scaling tests. For biomass per plant and earmass per plant, high statistical significance was detected in the C and D scaling tests, at this site. The significance of C scaling test showed evidence for C dominance x dominance type of epistasis while the significance of D scaling test provided evidence for I (additive x additive) gene interaction. The B and D scaling tests were significant in single plant harvest index at ORIBI. The A and B scaling tests were significant for reproductive tillers per plant and for single plant HI at ART, providing evidence for the presence of I (additive x additive), j (additive x dominance) and l (dominance x dominance) gene interaction (see Section 2.3.1).

4.6.4 Joint scaling tests

4.6.4.1 Estimates of additive, dominance and environmental effects

Results of a completely additive-dominance model (ADM) including the environmental effects are presented in table 4.32, which includes the Chi-square tests with 6df for testing the validity of those models. Both the additive and dominance gene effects were small in magnitude, but statistically significant in the case of plant height ($P<0.001$), earmass per plant ($P<0.001$) and plant harvest index ($P<0.001$). The absolute value of additive gene effects was twice that of dominance gene effects for plant height. Significant environmental, and in all cases environment x dominance (gh) interaction effects were detected. Additive x environment (gd) interaction effects were observed in plant height, productive tillers and in plant HI. All these additive – dominance models (ADM) were statistically significant, indicating their inadequacy in explaining the full cause of genetic variation .

4.6.4.2 Estimates of digenic epistatic gene effects and the environmental effects

The significance of the individual scaling tests, the inadequacy of the additive – dominance plus environmental effects model and the interaction of environment with the additive and dominance gene effects, necessitated the fitting of the full digenic epistatic gene effects plus environmental effects models. Estimates of this model including Chi – square test with 5 df for testing the adequacy of the model, are also presented in Table 4.32.

Insert table 4.32

As was the case with the ADM, the environmental effects on all the five single plant characters were significant (P<0.001). Additive gene effects, though small, were again detected for plant height, earmass per plant and single plant HI. Very large and significant (P<0.001) dominance gene effects were encountered for biomass per plant and earmass per plant. Plant harvest index and plant height showed small but statistically significant (P<0.001) dominance gene effects. One or more digenic epistatic gene effect was statistically significant in all of these models, indicating the presence of epistasis in the characters under study. All these models were rendered inappropriate by showing significance in the model Chi – square tests.

4.6.4.3 Perfect fit digenic epistatic gene effects at individual locations

The presence of significant environmental effects in the full digenic epistatic models fitted across the two locations necessitated reviewing of these models at individual locations. These were perfect fit models with no reserve degrees of freedom for the Chi – square test of the validity of those models. The estimates from fitting these models are presented in Tables 4.33 and 4.34. Relatively large significant (P<0.001) additive gene effects were detected for plant height per plant at both locations. They were small but significant for earmass per plant, reproductive tillers per plant and for HI per plant. Large dominance gene effects were encountered at ORIBI for biomass per plant, earmass per plant and, to a lesser extent in productive tillers and HI. High dominance gene variation was also evident for biomass per plant and productive tillers per plant at ART. All the five single plant characters showed significant epistatic gene effects at ORIBI. Productive tillers and harvest index are the only characters which showed significant epistatic gene variation at ART.

Table 4.33 Estimates of gene effects and their standard errors for different characters based On digenic epistatic model and heritabilities in the broad sense (H^2) and in the narrow sense (h^2) in a spring wheat cross (Sengwa x Nata) grown in winter 1994 at ART

Genetic parameter estimated	Plant height (cm)	Biomass per plant (g)	Earmass per plant (g)	Productive tillers per plant	Single plant harvest index (%)
M	84,6 ± 2,01	49,3 ± 7,04	32,0 ± 4,37	10,7 ± 1,54	65,1 ± 3,15
[d]	-8,2 ± 0,20***	-0,3 ± 0,83ns	2,6 ± 0,54***	0,6 ± 0,18***	4,6 ± 0,27***
[h]	5,0 ± 4,69ns	40,6 ± 17,07*	18,4 ± 10,57ns	13,8 ± 3,66***	-12,6 ± 6,49ns
[l]	-1,6 ± 2,00ns	12,4 ± 6,99ns	7,1 ± 4,34ns	3,6 ± 1,50*	-1,9 ± 3,14ns
[j]	-1,5 ± 1,13ns	1,7 ± 4,51ns	2,0 ± 2,79ns	0,5 ± 0,97ns	1,0 ± 0,82ns
[l]	-1,5 ± 2,77ns	-16,4 ± 10,58ns	-5,3 ± 6,55ns	-8,1 ± 2,27***	8,8 ± 3,39**
Espistasis	D	D	D	D	D
Heritability					
H^2	0,59	0,67	0,75	0,72	0,45
h^2	0,48 ± ,03***	0,26 ± ,16	0,41 ± ,14*	0,33 ± ,15	0,61 ± ,13*

*, **, *** = statistically significant at the 5%, 1% and 0,1% probability levels, respectively,
ns = not significant at 5% probability level.

M = mid-parent estimate

[d] = estimate of additive gene effects

[h] = estimate of dominance gene effects

[l] = estimate of pooled additive x additive gene effects

[j] = estimate of pooled additive x dominance gene effects

[l] = estimate of pooled dominance x dominance gene effects

Table4.34: Estimates of gene effects and their standard errors for different characters based on digenic epistatic model and heritabilities in the broad sense (H^2) and in the narrow sense (h^2) in a spring wheat cross (Sengwa x Nata) grown in winter 1994 at ORIBI

Genetic parameter estimated	Plant height (cm)	Biomass per plant (g)	Earmass per plant (g)	Productive tillers per plant	Single plant harvest index (%)
M	92,4 ± 1,90	2,5 ± 9,84	-2,5 ± 6,78	6,6 ± 1,57	59,1 ± 1,75
[d]	-10,4 ± 0,19***	-1,3 ± 1,63ns	2,4 ± 1,17*	2,7 ± 0,24***	3,5 ± 0,23***
[h]	-9,8 ± 4,47*	183,7 ± 24,68***	132,9 ± 17,22***	17,0 ± 3,81***	16,3 ± 4,32***
[l]	-7,3 ± 1,89**	99,1 ± 9,7***	71,6 ± 6,68***	11,6 ± 1,55***	8,4 ± 1,74***
[j]	2,7 ± 1,10*	-11,1 ± 7,20ns	-12,5 ± 5,13*	-2,2 ± 1,04*	-4,0 ± 1,19***
[l]	5,7 ± 2,68*	-103,1 ± 15,53***	-79,9 ± 10,88***	-7,1 ± 2,36**	-15,3 ± 2,69***
Espistasis	D	D	D	D	D
Heritability					
H^2	0,55	0,55	0,66	0,62	0,67
h^2	0,31 ± 0,03***	0,23 ± 0,16	0,54 ± 0,13***	0,59 ± 0,13***	0,63 ± 0,13***

*, **, *** = statistically significant at the 5%, 1% and 0,1% probability levels, respectively,
ns = not significant at 5% probability level.

M = mid-parent estimate

[d] = estimate of additive gene effects

[h] = estimate of dominance gene effects

[l] = estimate of pooled additive x additive gene effects

[j] = estimate of pooled additive x dominance gene effects

[l] = estimate of pooled dominance x dominance gene effects

4.6.4.4 Estimates of the non – genotype x environment digenic epistatic model

The non genotype x environment interaction model which estimates the genotype x environment interaction for each genetic effect in the full digenic epistatic model, was fitted to ascertain the environmental effects on the epistatic variation. Moreover, the digenic epistatic effects model fitted across sites had shown large environment effects and was proven inadequate. Estimates of

the effects of the fully expanded non genotype x environment interaction model are presented in Table 4.35. Additive gene effects were again large and statistically significant (P<0.001) for plant height. They were small but significant (P<0.001) for earmass per plant, productive tillers and plant HI. Dominance gene effects were large and statistically significant for biomass per plant, earmass per plant and productive tillers. Epistatic gene effects and their interaction with the environment were significant for all the five single plant characters. Small but significant (P<0.001) additive gene effects x environment interaction were observed for plant height and productive tillers, and also for HI (P<0.05). Environment x dominance gene effects interaction was large and significant for plant height (P<0.05), biomass per plant (P<0.001), earmass per plant (P<0.001) and single plant HI (P<0.05). This was another perfect fit model without chi–square test for goodness of fit. The preponderance of gene effects by environment interactions indicated a high degree of instability of the gene effects across environments.

4.6.5 Estimates of broad sense heritabilities (H^2bs) and narrow sense heritabilities (H^2ns) of the five single plant characters in the two locations

In Tables 4.33 and 4.34, estimates of broad-sense heritabilities (H^2) were moderate to high, at both sites for all the five single plant traits studied. Narrow-sense heritability estimates were low to moderate (0,48 and 0,31) for plant height, biomass per plant (0,26 and 0,23), for earmass per plant (0,41 and 0,54), for productive tillers per plant (0,33 and 0,59) and for single plant HI (0,61 and 0,63), at ART and RA, respectively, for the five traits. Thus plant HI, plant height and earmass per plant had the highest narrow-sense heritability estimates and biomass per plant had the smallest narrow-sense heritability estimates.

Table 4.35 Estimates of genetic, environmental and interaction effects and their standard errors, based on a digenic epistatic model, for different characters measured in a spring wheat cross (Sengwa x Nata) grown in winter 1994 at ART and ORIBI

Genetic parameter estimated	Plant height (cm)	Biomass per plant (g)	Earmass per plant (g)	Productive tillers per plant	Single plant harvest index (%)
M	89,0 ± 1,38	28,8 ± 5,92	15,2 ± 4,01	8,6 ± 1,09	61,3 ± 1,81
[d]	-9,3 ± 0,14***	-0,8 ± 0,92ns	2,5 ± 0,64***	1,6 ± 0,15***	4,1 ± 0,18***
[h]	-3,5 ± 3,24ns	104,9 ± 14,66***	74,4 ± 10,04***	15,5 ± 2,65***	3,4 ± 3,91ns
[l]	-4,9 ± 1,38***	53,0 ± 5,86***	38,9 ± 3,96***	7,6 ± 1,08***	4,1 ± 1,80*
[j]	0,6 ± 0,79ns	-4,5 ± 4,24ns	-5,2 ± 2,92ns	-0,8 ± 0,71ns	-1,5 ± 0,72ns
[l]	2,7 ± 1,93ns	-55,3 ± 9,18***	-41,7 ± 6,31***	-7,71 ± 1,64***	-3,9 ± 2,17ns
e	-3,9 ± 1,38ns	22,2 ± 5,92***	15,6 ± 4,00***	2,2 ± 1,10ns	1,6 ± 1,81ns
gd	1,1 ± 0,014***	0,5 ± 0,92ns	0,1 ± 0,64ns	-1,1 ± 0,15***	0,5 ± 0,18*
gh	7,3 ± 3,24*	-68,5 ± 14,66***	-52,9 ± 10,01***	; -2,0 ± 2,66ns	-11,4 ± 3,91*
gi	2,8 ± 1,38ns	14,2 ± 5,86***	-30,6 ± 3,95***	-4,1 ± 1,09***	-3,8 ± 1,80ns
gj	-2,1 ± 0,79**	6,3 ± 4,24ns	7,1 ± 2,92*	1,3 ± 0,71ns	2,5 ± 0,72ns
gl	-3,6 ± 1,93ns	41,4 ± 9,18***	34,6 ± 6,29***	-0,3 ± 1,65ns	10,4 ± 2,17***

*, **, *** = statistically significant at the 5%, 1% and 0,1% probability levels, respectively,
ns = not significant at 5% probability level.

M = mid-parent estimate

[d] = estimate of additive gene effects

[h] = estimate of dominance gene effects

[l] = estimate of pooled additive x additive gene effects

[j] = estimate of pooled additive x dominance gene effects

[l] = estimate of pooled dominance x dominance gene effects

e= estimate of environmental effects

gd= estimate of enviroment x additive gene effects

gh= estimate of enviroment x dominance gene effects

gi = estimate of enviroment interaction with additive x additive gene effects

gj = estimate of environment interaction with additive x dominance gene effects

gl = estimate of environment interaction with dominance x dominance gene effects

4.6.6 Single plant character associations

The phenotypic (rp) and genotypic (rg) correlation coefficients among single plant traits; plant height, biomass, earmass, productive tillers and HI, are presented in Tables 4.36 and 4.37 for the two locations. Phenotypic and genotypic correlations between plant height and biomass per plant were strong and significant (P<0.001) at ART (rp= 0.54; rg= 0.76) and at ORIBI (rp= 0.39; rg=0.67). These relationships were also strong and significant (P<0.001) between plant height and earmass per plant at ART (rp= 0,54; rg= 0,69) and also at ORIBI (rp= 0.37; rg= 0.78). Plant height was generally weakly correlated with both productive tillers and plant HI, except for the positive phenotypic correlation recorded between itself and productive tillers (0.36; P<0.001) at ART, and between itself and HI (0,53; P<0.01) at ORIBI. Biomass per plant was very strongly and significantly (P<0.001) correlated with earmass per plant at both locations (rp = 0.97; rg= 0.99 at ART and rp= 0.99; rg= 1 at ORIBI). Phenotypic correlation between biomass and HI was non significant at both locations but a significant (P<0.01) weak negative genotypic correlation (-0,32) was observed between these two attributes at ORIBI. Biomass and earmass per plant were positively significantly (P<0.001) correlated with productive tillers (rp = 0,79 to 0,84) (rg = 0,78 to 0,98), but very weak and non significant correlations were obtained between productive tillers and harvest index.

Insert table 4.36 and 4.37

5. DISCUSSION

5.1 Evaluation of selection criteria

The six F2-derived populations and their six constituent parents of diverse origin constituted a sound biological sample upon which reliable inferences on relative effectiveness of the different selection criteria could be made. Effective stratification of the six populations into uniform short-statured and tall-statured sub-populations was achieved in the F4 generation, enabling the subsequent determination of the selection criteria appropriate for use in the different plant height strata.

5.1.1 Grain yield performance of accessions and parents

The large variation in grain yields (8,6 - 10,8 Tonnes/ha) among the accessions, non significant variety x site interaction and the low coefficients of residual variation (c.v. < 8 percent), provided an optimum opportunity to compare the relative effectiveness of the different selection criteria in the selection of high yielding wheat genotypes. Similarity of mean grain yields between the short height and the tall height strata enabled unbiased comparison of the effectiveness of the different selection criteria between the two plant height strata. Mean grain yields of accessions were similar to the mean grain yields of the parents in four out of the six populations, implying preponderance of additive gene action in the expression of grain yield. In a way this denoted that sampling from the original population was unbiased and representative.

The superiority of grain yield performance of accessions selected on the basis of high single-ear progeny biomass or earmass (HEM) over that of accessions selected on the basis of low biomass

or earmass (LEM) of single-ear progenies, in the short height stratum of the five populations meant that HEM was an effective selection criterion for high grain yield among short statured genotypes. This result is consistent with those of Kramer *et al*.(1982) who found grain yield of hill plots to be strongly correlated with that of large plots, recognising that the single-ear progeny plots used in this study, resembled the hill plots in their study.

Accessions selected on the basis of high single-ear progeny harvest index (HHI) were superior in grain yield performance to the accessions selected on the basis of low harvest index (LHI) in only two of the six populations, for the short height stratum and in three populations for the tall height stratum. This apparent lack of consistency in the utility of HI, as an indirect selection criterion for grain yield would render it unreliable. This result is different from that of Fischer and Kertesz (1976) who found stronger correlation ($rp = 0.91$; $P<0.001$) between HI of microplots and grain yield of large plots than the correlation ($rp = 0.67$; $P<0.001$) between grain yield of microplots and grain yield of large plots, in spring wheat genotypes which were not classified into different plant height strata. The small genetic variance of HI in the wheat genotypes evaluated in this study may have caused the limited correlated response of grain yield to HI seletion.

5.1.2 Variation and means of single-ear progeny plot traits; biomass, earmass, HI and plant height

The three single-ear progeny plot traits; biomass, earmass and HI were generally associated with significant site x variety interactions. This may be due to the previously reported relationships that non-genetic differences are considerably greater in spaced than in close plantings (Harper, 1965; Nass, 1978). These interactions were however not confounding because they were predominantly due to variation in the degrees of differences rather than due to cross overs in

varietal performances. Thus the differences between the high selection groups and the low selection groups were not masked. This nature of genotype x location interaction has important practical implication that selections of such characters at one location become representative of a wide range of environments.

The significant differences between means of high phenotypic groups and low phenotypic groups of single-ear progeny traits; biomass, earmass and to a lesser extent HI, illustrate the success which was achieved in the separation of the high and the low phenotypic groups in each trait. For biomass, this result is consistent with those of Sharma (1993) who obtained high realised heritabilities in this trait.

The seven to fourteen percent greater mean single-ear progeny biomass and earmass in the tall height stratum of the populations than in the short height stratum may be explained by the generalisation that tall plants possess higher biomass than short statured ones (Nizam Uddin and Marshall, 1989). It also follows for single-ear progeny earmass as has already been shown in this study (section 4.4.3), that biomass was highly positively correlated with earmass. Furthermore, tall wheat plants tend to bear longer and larger panicles than short statured ones in spaced plantings. The reported differences in the expression of single ear progeny biomass and earmass substantiate the need to stratify the base populations into uniform plant height classes to maximise the utility of the two selection criteria.

Single-ear progeny plot HI was negatively correlated with plant height in three out of the six populations. This is in accordance with several findings in which HI was found to be higher in short statured plants than in tall statured ones (Donald and Hamblin, 1976; Fischer and Quail, 1990). The genetic explanation as given by Mather and Jinks (1971) may be the incomplete

dispersion of increasing alleles for HI between the constituent parents, or rather the association of the increasing alleles conferring high HI in the shorter statured parents. In any case, the semi-dwarf genes (Rht1 and Rht2) which may be present in the short statured genotypes are associated with high HI (Gale, 1979; Gale *et al*.,1981; Fischer and Quail, 1990).

In the analysis of variance of plant height of wheat accessions, the Short vs Tall accessions source of variation was significant in all the populations, whereas that among short or tall was mostly nonsignificant. Furthermore the accessions within the short height stratum of the six populations were much shorter (80cm) than the accessions in tall height stratum (94,5cm). This meant that stratification of the basic populations into the two plant height classes; the short height stratum and the tall height stratum was effective. This result renders confidence in the stratification of wheat breeding populations and possibly of other cereal plant species into different plant height classes in and after the mid-segregating generations, and confirms the preponderance of additive gene action in the expression of plant height in this plant species.

5.1.3 Entry-mean heritability estimates and genetic coefficient of variability of grain yield in experiment 1 and single-ear progeny attributes in experiment 2

The heritability in the broad-sense or rather the degree of genetic determination (Allard, 1960) is relevant in mass selection where individuals are selected out of the population on the basis of their phenotypic expression. In the case of this study, in which selection was among homozygous lines, selection operated on the total genetic variance which in turn only comprised the additive genetic variance and the additive type of epistatic variance (Dudely and Moll, 1969). It follows that when the additive x additive epistatic variance is small, the broad-sense heritability estimates

the narrow-sense heritability, in a heterogeneous population of inbred lines. The heritability co-efficient measures the proportion of variability which is attributable to genetic causes. As the value of heritability increases the expected advance from mass selection approaches the rate of genetic gain which would be obtained where the true genotype of every individual in a population is known (Lerner, 1958).

Greater entry-mean heritability estimates of single-ear progeny biomass and earmass than those of the responding trait, grain yield, in all the three plant height classes, meant that mass selection would be more effective in the two auxiliary traits than in grain yield *per se*. This result would increase the efficiency of the two auxiliary traits in the indirect selection of grain yield if the respective genotypic correlation between each of them and the responding trait, grain yield, is strong.

The high standard errors which were usually associated with very low estimates of entry-mean heritabilities of the single-ear progeny traits and of grain yield arose from the lack of robustness of this statistic as stated in section 4.1.2. The precision of the moderate and high estimates of entry-mean heritabilities as were frequently encountered in single-ear progeny biomass and earmass was appreciably high, rendering reliability in the application of those estimates.

Entry-mean heritability estimates were highest in the unstratified populations since they contain the greatest genotypic variation. Hence the genetic coeffients of variation were also highest in this plant height class. For single-ear progeny biomass and earmass entry-mean heritability estimates were reduced slightly in the short height stratum but were reduced further for biomass in the tall height stratum. This meant that genetic variance was lower in the tall height stratum than in the short height stratum for single-ear progeny biomass.

Thus efficiency of mass selection for single-ear progeny biomass would be expected to decrease with increase in plant stature and remain similar across plant stature for single-ear progeny earmass.

The reported entry-mean heritability esimates for single-ear progeny biomass and earmass are not unusual. Kramer *et al.* (1982) used slightly bigger plot sizes than those in this study and also obtained high entry-mean heritability estimates (0,81) for biological yield. Amin *et al*. (1992) also obtained a high entry-mean heritability estimate for biomass (0,70) in a similar study with durum wheat. Recently, Sharma (1993) obtained realised heritability estimates, which were greater (0,49 to 0,85) at higher fertility than at low fertility (0,22 to 0,44). The high entry-mean heritability estimates for single-ear progeny plot earmass are comparable to those obtained by Kramer *et al*.(1982) and Amin *et al.* (1992) for grain yield.

The low to moderate entry-mean heritability estimates which were obtained for HI imply that the wheat genotypes which were studied vary little in HI. One possible reason for this outcome is that CIMMYT derived semi-dwarf wheat germplasm possesses a high HI (Waddington *et al*., 1986). Moreover HI was subject to high environmental variation. Similarity of entry-mean heritability estimates (which were generally low in both traits) between single-ear progeny HI and the responding trait, grain yield, would render HI ineffective as an indirect selection trait for grain yield performance.

The observed range of entry-mean heritability estimates for single-ear progeny HI is similar to that reported by Rosielle and Frey (1975) (0,35 to 0,66) for HI in oat lines derived from a bulk population, and is also somewhat similar to the realised heritability values (0,44 to 0,60) which were obtained by Sharma and Smith (1986) in winter wheat. The entry-mean heritability estimates for HI in the study of Kramer *et al.* (1982) and Amin *et al.* (1992) were in contrast high,

being 0,98 and 0,80. Batt (1977) also found high realised heritability estimates for HI (0,76 - 0,88) using early segregating generations of spring wheat.

Low entry-mean heritability estimates for HI in some of the populations in this study, are consistent with the results of Londero *et al.* (2000) who found low realised heritability (0,31) for biological yield for bread wheat in Argentina.

Entry- mean heritability estimates may be biased upwards by genotype x environment interaction i.e. genotype x location, genotype x year or genotype x location x year, leading to erroneous conclusions as discussed by Johnson *et al.* (1955). Significant genotype x environment interactions were reported for both grain yield and harvest index by Sharma *et al.* (1978) in Oklahoma (USA) and by Ellison *et al.* (1984) in Australia. Small but significant genotype x location interaction variance was measured in the three single ear progeny traits; biomass, earmass and harvest index and also in two populations for grain yield in this study. Contribution of variation due to season and its interaction with genotype and location are expected to be minimal in Zimbabwe in which weather conditions of production in the dry winter months under irrigation are fairly stable. Since the genotype x location interaction in single-ear progeny biomass and earmass were of simple non cross over type, the genotypic ranks in these traits were not affected across the different locations. This strengthened the reliability of these two auxiliary traits in predicting grain yield performance of wheat over a wide range of environments.

Estimates of broad sense heritability as a ratio of genotypic to phenotypic variance indicate the effectiveness with which selection of genotypes can be based on phenotypic performance, but provide no indication of the amount of genetic progress that would result from selecting the best individuals (Johnson *et al.,* 1955). Their utility increases when they are used in conjunction with

the selection differential such that the genetic advance is predicted as the product of the heritability ratio and the selection differential.

In this study, it was most appropriate to combine heritability ratios with the genetic coefficient of variability following the suggestion of Burton (1952), to facilitate the comparison of genetic variability in the various populations and over the different plant height strata.

High values of entry-mean heritabilities were, in this study, associated with high values of genetic coefficients of variability. Since the mean G.C.Vs were much greater for single-ear progeny earmess and biomass than for grain yield in all the plant height classes, indirect selection for grain yield using the single-ear progeny earmass and biomass would be more justified than direct selection. The results imply that there was ample scope to select for single-ear progeny earmass in both the short height and the tall height strata of the populations. For single-ear progeny biomass and grain yield, the scope of selection decreased with increasing plant stature since the genotypic variance generally decreased with increasing plant stature of genotypes. On the other hand, the scope of selecting for HI increased with increasing plant stature since the G.C.Vs were generally higher in the tall height stratum than in the short height stratum. This appears logical because short statured genotypes tend to possess higher HI than tall statured ones (Gale, 1979), thus genetic variability among short genotypes is expected to be small. It should be noted that some wheat populations gave high G.C.Vs in the tall height stratum for biomass yield and grain yield. Thus genetic variability in either HI in the short height stratum, or biomass and grain yield in the tall height stratum, may be specific to the wheat crosses being studied.

5.1.4 Association between grain yield performance of wheat accessions and their respective single ear progeny traits

The functional relationship between the selection traits i.e. biomass, earmass and harvest index of single-ear progenies and the responding trait, which in this case is the grain yield of wheat at standard seed rates, is in terms of the genetic correlation, the main determinant in correlated response to selection (Lerner, 1958; Falconer, 1981). The magnitude of the heritability coefficient of the selection trait relative to that of the responding trait and the selection intensity are the other factors determining the degree of the correlated response which may be achieved (Falconer, 1981; Searle, 1965).

In this study, there appeared to be structured associations between attributes of single ear progenies and grain yield in commercial stands with respect to different stature of genotypes. The idea of observing the relationships in different plant height strata was to elucidate the differences in relationships of single ear progeny plot characters with grain yield of wheat in commercial stands, as influenced by plant stature. Discrimination in the utility of biomass and harvest index of spaced plants as selection criteria for high yielding genotypes in different plant height strata was first ascertained by McVetty and Evans (1980) who noted that biomass was more effective in tall statured genotypes, while harvest index was more appropriate in the short statured genotypes. In view of these findings, the present study aimed to ascertain which, among the three single ear progeny attributes, is most strongly correlated with grain yield performance of wheat genotypes in different plant height strata. These results would form the basis of designing appropriate selection criteria or indices for yielding ability in genotypes of different stature.

McVetty and Evans (1980) did not measure the correlation of grain yield of spaced plants with grain yield of wheat in standard seed rates. Furthermore, they used spaced plants and not single-ear progeny plots. This may account for the differences in their conclusions with those of the present study. The strong phenotypic correlations between earmass of single-ear progenies and grain yield of wheat which were obtained in the short height stratum (rp= 0,71; P<0.001 to 0,91; P<0.001) of five out of six populations and to some lesser extent in the unstratified populations (rp= 0,40; P<0.001 to 0,57; P<0.01) is consistent with the findings of Sharma and Smith (1987) between grain yield of very low seed rates and grain yield of standard seed rates. The results of Kramer *et al.* (1982) were even higher (rg = 0,82) for hill plots of almost similar size, but with a narrower inter-row spacing (40cm). The latter found the widening of inter-row spacing from 20cm to 40cm to strengthen the correlation between hill plot grain yield and grain yield at standard spacing. The inter-row spacing in the single-ear progeny plots in experiment 2 of this study was even wider (60cm) and was expected to improve the relationship even further by minimising the competition among neighbouring genotypes.

Fischer and Kertersz (1976) in a similar experiment with spring wheat genotypes in North West Mexico, used slightly larger and more closely spaced microplots (3 row, 3m long, 20cm apart) compared to the single row plots of this experiment. They still found a significant positive correlation between grain weight of microplots and large plot grain yield (rp =0,67), which is similar in magnitude to the average figure in the correlation between earmass of single ear progenies and large plot grain yield in the current study. Their study did not discriminate between the relationships in the different plant height strata and gave a higher correlation (rp = 0,91) between harvest index of microplots and commercial grain yield than that between the respective grain yields of plots of different sizes.

In the current study, biomass of single-ear progenies was positively phenotypically correlated with commercial grain yield (0,44 to 0,77; P<0.01) in the short height stratum. These correlations were smaller than those of earmass with grain yield. Biomass of single-ear progeny plots was, however, expected to have a similar relationship with commercial grain yield to that of earmass, since these two attributes were very strongly positively correlated. Positive and strong association between biomass of microplots and grain yield of large plots of wheat was also reported by McVetty and Evans (1980) among tall statured wheat genotypes only. Other similar reports were given by Geleta *et al.* (1991) in Ethiopia for rain fed wheat and by Sharma (1993) in spring wheat grown in a cultural environment similar to that in Zimbabwe. Londero *et al.* (2000) also found biomass of sparsely seeded microplots to be more predictive of spring wheat cultivar performance than harvest index in Argentina.

The apparent lack of association between single ear progeny harvest index and large plot grain yield (rp = 0,01 to 0.66; P<0.01) in this study is inconsistent with several findings in which HI was significantly positively correlated with grain yield, with rp values ranging from 0,62 to 0,96 (Syme, 1970, 1972; Nass, 1973; Fischer and Kertersz, 1976; Batt and Derera, 1978; Ellison *et al.*,1985; Sharma and Smith, 1987; and Amin *et al.,* 1992). One of the possible reasons for lack of grain yield response to harvest index selection in this study may be the low selection differential for this trait in the material under study. It may be reasoned that the yield of wheat in the Zimbabwean intensive culture under irrigation, in the cool winter months, is more a function of rapid biomass accumulation in combination with a high grain filling rate (Mashiringwani, 1993) rather than harvest index *per se*. In any case, harvest index was found to be negatively correlated with biomass in this study (Tables 4.34 to 4.36) and in several others (Donald and Hamblin, 1976; Fischer and Kertersz, 1976; Sharma and Smith, 1986; Geleta *et al.,* 1991, Sharma, 1993 and Londero *et al.,* 2000).

The genotypic correlations between single-ear progeny traits and grain yield in trials which are presented in Tables 4.21 to 4.23 were in certain cases greater than unity. This is not unusual according to Bos (1981), who ascribed such a result to the estimation of rg (the genotypic correlations) using heritability estimates which are unrobust and subject to sampling errors. Such estimates were constrained to the realistic values of 0,99.

5.1.5 Interrelationships of single-ear progeny traits.

It was important in this study to ascertain the mutual associations among single-ear progeny traits; biomass, earmass, HI, and plant height, over different plant stature. This knowledge would give insight on the nature of correlated responses of the remaining traits when one or more of them are under selection. For instance, the moderate to very strong phenotypic (0,38; $P<0.01$ to 0,83; $P<0.001$) and genotypic (0,40; $P<0.01$ to 0,99; $P<0.001$) correlations which were obtained between single-ear progeny biomass and earmass in the unstratified populations and in the short height stratum of the populations indicate that these two traits strongly positively covary. That their relationship tended to weaken with increasing plant stature, partly explains the negative relationship that was encountered between biomass and HI of single-ear progenies.

Harvest index was consistently positively correlated with earmass ($rp= 0,24$; $P<0.05$ to 0,81; $P<0.001$)($rg= 0,30$; $P<0.05$ to 0,96; $P<0.001$) across the plant height classes. Thus the apparent absence of correlation or the negative association between biomass and harvest index arose from the proportionally higher increments in biomass than in earmass, given that biomass and earmass are cofactors of the harvest index ratio. Furthermore, the positive concomitant variation between biomass and earmass may have contributed to the weak associations between the grain yield and harvest index in the different strata of the populations. That single-ear progeny biomass and

earmass were positively correlated with plant height, is expected because tall plants yield more phytomass and bear larger panicles in spaced plantings than short statured ones. The weak or negative relationships which were encountered between plant height and harvest index corroborates the already reported findings (Gale, 1979; Fischer and Quail, 1990), but it must be noted that one or two populations gave positive phenotypic and genotypic correlations between these two traits in all the three plant height classes. Thus certain wheat crosses may possess both large variation and magnitudes of HI in the tall height stratum.

In practical breeding and selection strong positive correlation which were found between biomass and earmass is desirable, since the selection of the easily measurable earmass leads to correlated responses to biomass which has been found to contribute to high grain yield of wheat (Sharma, 1993). The same can be said for the strong positive correlation which was found between earmass and HI, with particular reference to the tall statured wheat genotypes, in which HI seemingly confers high grain yield potential. It is worth noting that selection for high HI in the tall wheat genotypes may not ensure high biomass, since these two attributes were found to be negatively correlated in the tall height stratum. This study provided insight on the changes in mutual associations among the single-ear progeny traits as influenced by plant stature. This knowledge is helpful in the formulation of appropriate selection indices in the different plant strata.

5.1.6. Relative selection efficiency of single-ear progeny traits; biomass, earmass and harvest index

Improvement of grain yield in wheat through yield component selection such as spike, spikelet and kernel parameters *per se*, has been rendered ineffective due to the presence

of genotype x environment interaction (McGinnis and Shebeski, 1968; Knott, 1972). The narrow sense heritability or additive genetic variance for these characters are low relative to environmental error variation (Fischer and Kertesz, 1975). Other reasons for failure of yield components as selection criteria for grain yield performance of wheat at standard spacing are ascribed to the presence of allometric relationships in cereals (Donald, 1968; Grafius *et al*.,1976). This is where competitive advantage of genotypes vary over different plant spacings, with different genotypes being favoured as the competitive environment changes. Component compensation, which is also subject to genotypic variation, has been reported by Sharma (1993) to distort relationships between yield components and grain yield potential in different plant spacings. Furthermore, the negative relationship between yield components such as number of grains and average individual grain weight (Fischer *et al.,* 1977; Gale 1979; McClung *et al.,* 1986 and Borrel *et al.,* 1991), hampers progress in the use of these criteria in the selection for high grain yield in wheat.

The use of morpho-physiological selection criteria such as biomass, earmass and harvest index of single ear progeny plots, which in this study were mutually widely spaced to reduce alley border competition effects, and which were also stratified into uniform plant stature, attempted under limitation of seed and space to simulate to some degree, the competitive environment of a wheat crop.

Indirect selection gives speedier improvement than direct selection when the genetic correlation is greater than the square root of the heritability of the responding trait (Searle, 1965) i.e. when

$$rg > h_y$$

In the case of this study in which the genetic correlation has been calculated as the ratio of the phenotypic correlation over the geometric mean of the heritabilities of the selection trait and the responding trait ($rp/h_x h_y$), selection for grain yield through single ear progeny traits is more effective than direct selection for yield when the phenotypic correlation coefficient (rp_{xy}) between grain yield and the auxiliary trait is greater than the heritability coefficient of the responding trait (h_y^2) (grain yield), i.e. when,

$$rp_{xy} > h_y^2 \quad .$$

Some of the RSE values obtained in this investigation were greater than unity because of very low heritability estimates in the responding trait, grain yield, relative to the phenotypic correlation coeffients between grain yield and single-ear progeny traits. Standard errors of some RSE values were large because, as explained by Searle (1965), because RSE was estimated using the ratio (h_x/h_y) which is not robust. Searle (1965) noted that (h_x/h_y) can differ quite markedly for small differences in the heritability estimates.

The relative merit of the different single-ear progeny traits; biomass, earmass and harvest index as indirect selection traits for high grain yield in spring wheat grown under irrigation, was in the following order in the different plant height strata;

earmass > biomass > harvest index in the short height stratum ($\leq$85cm),

earmass > harvest index = biomass in the tall height stratum (>85cm), and

earmass > biomass > harvest index in the intact populations without stratification into plant height classes.

This order of merit agreed with the degrees of phenotypic association between the auxiliary traits and the responding trait (grain yield) as was encountered in the different plant height strata of the six populations. The RSE values of the different indirect selection traits were also inversely related to the entry-mean heritability estimates of the responding trait, grain yield.

The significance of earmass of single-ear progenies in identifying to some appreciable degree, average and high yielding wheat genotypes under Zimbabwean high productivity conditions, corroborates the findings of Kramer *et al.* (1982), Fisher and Kertesz (1975) and those of Sharma (1993). The results from this study differ from those of McVetty and Evans (1980) who found harvest index of short statured spring wheat genotypes to be more indicative of grain yielding ability than grain mass or biomass of spaced plants. The higher HI selection differentials (HI range; 33% to 45%) in the genotypic material used by McVetty and Evans (1980) compared to the limited within population variance of HI in the material of this study, may account for the differences in the outcomes of these two studies. Moreover hill plots were used in this current study and not spaced-planted single plants as was the case in the earlier study. Biomass of single ear progenies appeared to be related to yielding ability of short statured wheat genotypes, probably due to its strong positive correlation with earmass in the hill plots. Biomass was however not as effective as earmass but was similar to harvest index, in the tall height stratum of the six populations. Moreover genotypic variance of biomass was generally smaller in the tall height stratum than in the short height stratum.

The semi-dwarf spring wheat genotypes which constitute the plant material used in this study mostly originate from the International Maize and Wheat Improvement Centre (CIMMYT) wheat germplasm, based in Mexico. This germplasm is known (Waddington *et al.*, 1986) to possess high harvest index. This may furnish the reason for the limited selection differential and hence the apparent lack of yield response when HI was used as a selection criterion in the short

height stratum. The subtle differences in grain yield response to various selection criteria are not only genetic, but also environment specific. Phenotypic and genetic correlations between grain yield and auxiliary traits has been known to vary over different plant stature in this study and those of McVetty and Evans (1980).

Coefficients of heritability of characters such as grain yield and the three single ear progeny traits, biomass, earmass and HI tend to change across environments thereby causing variation in both the correlated response and the direct response in grain yield. For instance, Sharma (1993) found higher realised heritabilities in biomass and grain yield in high fertility regimes than those obtained in low fertility regimes. In this study some populations yielded moderate heritabilities, G.C.Vs and positive correlations in both the short and tall height strata, implying that the strength of these genetic parameters may be specific to the wheat populations studied. It is worth noting that this study used elite x elite crosses, as typical of any applied programme. This meant less genetic variance than an academic study that could, for example use good x bad, to maximise the genetic variance.

Wheat grain yield response to indirect selection using microplot earmass and biomass in the intensive culture under irrigation, in Zimbabwe, may be explained by visualizing that in wheat, plump grain only arises when the source/sink ratio during grain filling is considerably higher than that giving maximum grain yield (Fischer *et al*.,1977). Thus a large biomass in terms of the photosynthetic factory, would ensure sufficient photosynthetic capacity to supply adequate photosynthate to fill to plumpness, a large number of grains, i.e. the sink. A large sink is in this case reflected as large earmass of single ear progenies. This hypothesis is further supported by the contention of Payne *et al*. (1986) who suggested that increasing biomass maybe necessary to achieve future increases in yield of cereals.

In high yielding environments, harvest index alone will not ensure high grain yield (Donald and Hamblin, 1976; Borojevic, 1983), since high biomass, (which has been found in this study and several others to be negatively correlated with HI) is also an important determinant of high grain yield. Kraljevic and Borojevic (1988) also noted that high harvest indices of the triple dwarf genes (Rht3) under the limited photosynthetic source and capacity, failed to confer high grain yields. However milder expressions of dwarfism as encoded by the Rht1 and Rht2 dwarfing genes have been found (Fischer and Quail, 1990) to express large number of kernels per spike and per m^2, without compromising biomass. This further explains the effectiveness of biomass and earmass of single ear progenies in predicting grain yield performance of short statured wheat genotypes in Zimbabwe.

The moderate response of wheat grain yield to harvest index selection which was encountered in the tall height stratum may have resulted from the slightly higher HI selection differentials in this stratum when compared with that in the short height stratum. Requirement for large sink strength (i.e. large earmass of single-ear progenies) was also evident in this stratum, since earmass as a selection criterion, was more effective than HI. Harvest index i.e. the number x weight of kernels over the total above ground biomass, is indicative of the efficiency of tall statured plants in converting total photosynthate into harvestable yield. Harvest index is for this reason expected to account for wide adaptation in yield of tall wheat genotypes across environments.

The processes which determine yield potential i.e. the transformation of solar energy into harvestable plant parts are conveniently divided into three major processes, first, the interception of incident solar radiation by the canopy, second, the conversion of the intercepted radiant

energy to chemical potential energy (i.e. plant dry matter), and third, the partitioning of the dry matter produced between the harvested parts and the rest of the plant (Araus, 1996).

The yield or harvested part (Y) of a crop over a given period of time, can therefore be simply expressed by the paradigm (Hay and Walker, 1989)

$$Y = Q \times I \times E \times H,$$

where Q is the total quantity of incident solar radiation received by the crop over the growing period, I is the fraction of Q intercepted by the crop canopy, E is the overall photosynthetic efficiency of the crop (i.e. the efficiency of conversion of radiant to chemical potential energy or the total dry matter produced per unit of intercepted radiant energy) and H is the harvest index. The quantity Q is uniform to all genotypes in the trial nursery, thus variation in dry matter between genotypes would arise from genotypic differences in I, E and H.

Indeed total biomass, which in this equation is represented by Q x I x E can be understood in the physiological sense, to be the consequence of crop photosynthesis over time. Thus increased crop photosynthesis in a wheat crop would be brought about by an increased interception (I) of the photosynthetic active radiation (PAR) by the canopy throughout the growing season (Araus, 1996). Harvest index can be achieved by a fast approach to full cover as exhibited by the short statured Zimbabwean wheat variety called SCAN (75cm tall) which has a spreading growth habit in its early vegetative phase, and also a profuse tillering and vigorous growth habit. Profuse tillering and vigorous growth habit are also characteristics of the other current high grain yielding cultivars viz SCEPTRE, SCOPE and SCHOLAR. All these cultivars have been selected on the basis of high biomass/earmass of single ear progenies. A greater duration of

photosynthetic organs as typified by the recent cultivar SC NDUNA, which apparently exhibits a stay green characteristic, may also increase (I), thus providing another source of variation in the final biomass attained among wheat genotypes.

Genotypic variation in the efficiency of conversion of (PAR) into dry matter, may arise through either differences in the canopy structure or differences in photosynthetic capacity of the photosynthetic organs, without any concomitant variation in area or duration of the photosynthetic organs. This may also account for variation in total biomass through variation in earmass among genotypes.

A spreading growth habit like that of SCAN would help it to maximally intercept the limited radiation during the relatively short days during the early vegetative phase (<11 hours in May in Zimbabwe). A progressively upright top foliage, including the flag leaf, later on during flowering and grain filling may be a useful canopy structure to maximise biomass accumulation under Zimbabwean conditions in which early growth is associated with cool relatively short days and progressive increases of day length and tempreture to maxima of 12 hours and $\pm 28^0$C respectively, at maturity.

The definition of Donald and Hamblin (1976) which gives the yield of cereals as

grain yield = biological yield x HI,

can be further interpreted in environments where grain yield shows dependence on biological yield as (Donald and Hamblin, 1976)

$$Ygr = KYbiol$$

Where, Ygr is the grain yield, the constant K represents harvest index and Ybiol is the biological yield. Under these situations grain yield rises as biological yield increases and further improvements in grain yield arise from selection for high biomass at constant HI (Borojevic, 1983). This is demonstrated in Tables 4.34 to 4.36 in this study where earmass was strongly correlated with biomas.

Earmass or grain yield of single-ear progenies showed the strongest positive correlations with grain yield of genotypes in replicated trials in this study. Earmass is the prime component of harvest index in the above equation of Hay and Walker (1989) and is the sink in the photosynthetic system under consideration. Earmass as a sink is further decomposed into components represented by the following paradigm of Slafer *et al.*(1994b);

earmass = number of spikes x spikelet/spike x grains/spikelet x weight/grain.

The number of spikes in a wheat crop is a function of seeding rate and tillering ability of the cultivar. Some cultivars are better able to maintain a high number of fertile tillers than others, over a range of cultural and environmental conditions (Sanford and Utomo, 1991). Hence those genotypes which maintain high tillering ability in both single ear progeny plots and in standard spacing, are likely to yield better than those which are sensitive to seeding rates. The number of spikelets per spike is in turn a function of the spike length and also the inherent ability of a genotype to develop and sustain a large number of grain under prevailing environmental conditions of temperature, photo-period, nutrition and moisture status.

Environmental stress factors such as high temperatures, long photo-periods and drought accelerate ear development or more specifically, reduce the duration of spikelet

production (DSP) thereby reducing the number of spikelets produced and ultimately the number of grains per m² (Allison and Daynard, 1975; Frank, Bauer and Black, 1978). Wheat genotypes differ in their response to these stresses, leading to differences in yield performance among them.

Allison and Daynard (1975) noted that some temperate or high latitude wheat varieties respond to shorter day length in Zimbabwe by producing a larger number of spikelets. Such germplasm may be useful in breeding for high spikelet production in Zimbabwe. The average optimum temperature for wheat development is 16ºC, which is experienced in the highveld (>1250m) areas of Zimbabwe between tillering and early grain filling stages of the wheat crops. The middleveld areas (900 - 1250m), and in particular, the lowveld areas (<900m) of Zimbabwe, and effectively all the Zimbabwean wheat production areas experience much warmer temperatures during late grain filling than those for optimum growth (Cackett and Wall, 1971). Fischer and Maurer (1976) found a 4% reduction in grain yield potential of a dwarf spring wheat variety in North West Mexico for every 10°C rise in temperature above the optimum range. Their results explain the lower wheat grain yields of the lowveld areas of Zimbabwe when compared to those obtained in the highveld areas. Fischer and Maurer (1976) and later Frank *et al*. (1978) established the causes of yield loss due to high temperature between tillering and early grain filling to be the reduction of grains/m^2 via changes in spikes/m^2 and grains /spikelet. High temperatures during late grain filling brought about reductions in kernel weight and also reduced the final grain yield.

In Zimbabwe, high yielding wheat genotypes would be those which tiller sufficiently to establish a large photosynthetically active biomass, and at the same time maintain a large number of grains without sacrificing grain weight, since grain weight is usually negatively associated with grain number (Fischer *et al*.,1977). It has been established that under Zimbabwean conditions, both

high grain yield and high test weight are maintained by those wheat varieties which have a high grain filling rate (Mashiringwani and Sweppenhauser, 1993) since such varieties are better able to fill the grain during the relatively cool period before the high rise in temperature with the onset of summer. Moreover, Alexander *et al.* (1984) reported kernel weight to be the most dependable yield component trait in the selection for grain yield potential in winter wheat crosses.

In this study, earmass of single-ear progenies appears to be strongly indicative of productivity of a genotype under the potentially high grain yielding environment of the cool highveld (>1250m) areas of Zimbabwe. When the single-ear progeny plots are adequately spaced apart (±60cm) as was the case in this study, this attribute seems to be little affected by both the alley border effects reported by Jensen and Federer (1964) and the allometric compensation problems described by Grafius *et al.* (1976) and by Gymer(1981) for grain yield components. In the context of this investigation, earmass of single ear progenies is representative of sink capacity of a wheat genotype and is reflective of a cultivar's ability to produce a large number of grains, and probably to a lesser extent its ability to bear heavy grains in the Zimbabwean highveld. This is further supported by the results of Mashiringwani (1988) in which grains per ear were strongly correlated with grains per square meter and also in which grains per ear were strongly correlated with grain weight per ear.

It is evident from the results of this study that short statured wheat genotypes (<85cm) can be selected on the basis of their expression of high single-ear progeny earmass. This indirect selection for grain yield performance would be most appropriate in near homozygous wheat genotypes, in the single-ear progeny generation when seed is still sufficient to conduct replicated trials. Furthermore this procedure would conserve resources by facilitating the culling of poor

yielding genotypes while identifying the average and the high grain yielding ones for further evaluation. The stability or maintenance of uniformity of genotypic ranks of single-ear progeny earmass across locations, which was obtained is this study, implies that effect of selection of this trait at one location would be applicable over a wide range of enviroments

Earmass of single-ear progenies can still be used in the indirect selection for grain yield among tall statured (>85cm) wheat genotypes, since it gave the highest number of high RSE values in the tall height stratum. Tall wheat genotypes are expected to benefit from their ability to mobilise photosynthate into grains i.e. from possessing high HI. It is therefore suggested that indexes involving earmass, HI and, perhaps biomass, be evaluated following the methods of Lerner (1958) and Baker (1976).

5.2. Inheritance of grain yield, biomass, harvest index, number of tillers per plant and plant height in a spring wheat cross.

Determination of genetic variation governing the expression of grain yield and its auxiliary selection traits, biomass, harvest index, plant height and number of productive tillers, was important in this study in that the information derived from here, would help in the formulation of effective breeding and selection strategies.

In the preliminary genetic analysis of the variation governing the expression of the five traits in a Sengwa x Nata spring wheat cross, the additive-dominance models failed to fully explain the total genetic variation as indicated by the statistically significant chi-square values for lack of fit of these models. The only exception was the character plant height at ART. This was further substantiated by the statistical significance of one or more individual scaling tests at both

locations; ART and ORIBI. These preliminary results suggested the presence of inter-allelic or epistatic genetic variation in all the five traits with the exception of plant height at ART. The expanded genetic variation analysis of each of the five single plant traits in the spring wheat cross Sengwa x Nata, will be discussed separately below.

5.2.1. Inheritance of plant height

The additive genetic effects towards shortness constituted the major component of genetic variation governing the expression of plant height at the cool location, ART. All types of epistatic genetic variation were small and statistically nonsignificant at this location. Significant dominance gene action was detected at this site. Large values of both heritability in the broad sense (0,59) and in particular that of the heritability in the narrow sense (0,48), indicated further the existence of relatively large additive gene effects.

Comparison of generation means for plant height at ART, suggested partial dominance of genes towards tallness as indicated by an F1 mean larger than the mid parent value but smaller than the taller (P2) parent, Nata. This is also shown by the smaller variance of the recessive parent backcross (which in this case is BC1) in relation to the magnitude of the variance of the backcross to the dominant parent (BC2). A similar deduction was made by Johnson *et al*. (1966) in a study on the inheritance of plant height in a hard red winter wheat cross. The degree of dominance D/H (0,637) which is less than unity provides further evidence of partial dominance and its similarity with the potency ratio of (0,61) is indicative of full association of genes controlling height between the two parents. In other words the dwarfing genes are in the shorter parent, Sengwa, and the genes for increased height are in the taller parent, Nata.

As was the case at ART, the additive gene effects towards shortness were again the most important in controlling the expression of plant height at ORIBI. This is shown by joint scaling tests on the generation means at ORIBI. Dominance gene effects operating towards shortness and being of similar magnitude but slightly smaller than the additive gene effects were observed at ORIBI. All the three digenic epistatic gene effects; additive x additive (i), additive x dominance (j) and dominance x dominance (l) were statistically significant at ORIBI. They were predominantly of duplicate type, since the [h] and [l] were, on balance of different sign (Mather and Jinks, 1971). The dominance and some of the epistatic gene effects were grossly unstable over the two environments as shown by the significant gene x environmental interaction effects (gh) and (gi) in the expanded model. The additive gene effects were fairly stable, showing very small but statistically significant (gd) effect. In this cross and in a previous study on the inheritance of plant height in wheat (Johnson *et al.*,1966), the fixable additive and additive x additive gene effects accounted for the major portion of genetic variation in plant height, making it a highly heritable character amenable to successful selection in the early segregating generations following crossing. The study by Ketata *et al.* (1976), however, showed a high contribution of dominance variance in the control of plant height and in this study, dominance gene effects were considerable but unstable over locations. Thus a fair amount of inbreeding, say to F4 generation, may be necessary to allow fixation of heterotic loci before selection.

5.2.2. Inheritance of Biomass

Biomass per plant was predominantly controlled by dominant gene effects which were associated with large additive x additive and dominance x dominance epistatic gene effects at both sites ART and ORIBI. Epistasis at both sites was of the recessive suppressor or duplicate type, which poses complexity in breeding. There was significant environmental influence on the genetic

effects which may have been inflated by the experimental errors in measuring biomass. Moreover, the dominance gene effects and the two epistatic gene effects were unstable in terms of the relative magnitudes over the two locations. This is shown by the statistical significance of (gh), (gi) and (gl), in the non genotype x environmental interaction model. Similar gene effects were measured for biological yield per plant in two spring wheat crosses by Srivastava *et al.*(1992) in an environment similar to that of the present study. Unlike the current experiment, however, Srivastava *et al*. (1992) reported small additive gene effects.

Positive mid-parent and better parent heterosis was obtained for biomass per plant at ART but these were both negative at ORIBI, substantiating the dependence of heterotic expression on environment as noted by Paroda and Joshi (1970) and Matzinger *et al.* (1959). The basis of heterosis in this cross is over dominant gene action and also most likely due to dispersion of the dominant genes between the constituent parents, which are of similar biomass. The low narrow sense heritabilities were due to the large dominance and epistatic genetic variance relative to the very small and non significant additive genetic variance. Single plant biomass surprisingly gave high broad sense heritabilities at both sites. Thus environment variance was relatively small compared to the total genetic variance.

The bulk handling of breeding populations would ensure ample genetic variability for final selection in the advanced generations when most or all the genetic loci are fixed.

5.2.3. Inheritance of Earmass

The mode of inheritance of grain yield or earmass per plant in this wheat cross, was almost similar to that described for biomass per plant. In the case of earmass per plant, however, small

but statistically significant additive gene effects were encountered at both ART and ORIBI and also in the non genotype x environment, full digenic epistatic model. These additive gene effects were similar to those obtained for grain yield per plant by Srivastava *et al*. (1992).

Dominant gene action was the most important in controlling the expression of earmass per plant, as was in the earlier studies of Johnson *et al.* (1966), Paroda and Joshi (1970), Ketata *et al*. (1976) and Srivastava *et al.* (1992). All the three types of digenic epistasis viz. additive x additive (i), additive x dominance (j) and dominance x dominance (l) gene action, governed the expression of earmass per plant. This epistatic genetic variation was predominantly of duplicate or recessive suppressor type as was encountered in the studies of Paroda and Joshi (1970), Ketata *et al.* (1976) and Srivastava *et al*. (1992). The dominant gene effects and all the epistatic gene effects were more pronounced at the warmer site, ORIBI, than at the cooler location, ART. This instability was evident in the statistical significance of the gene effects x environment interaction (gh, gi, gj, and gl).

Broad sense heritabilities were high, indicating the higher importance of the total genetic effects relative to those of the environment, on the trait. The presence of significant additive gene effects accounted for the presence of moderate narrow sense heritabilities.

The presence of some additive gene effects in earmass per plant means that improvement in this trait can be brought about by simple selection procedures, especially through an easily measurable or observable morphological trait which may be strongly genetically correlated with it. However, the large dominance and epistatic gene effects which also control the expression of grain yield would slow such progress and the suggestion of Gill *et al.* (1972) and Joshi (1979), of intermating of selects followed by visual selection in early segregating generations, would

simultaneously exploit both types of gene effects. Further, this approach is likely to break some undesirable linkages, resulting in the establishment of rare useful recombinations (Srivastava *et al*., 1992 after Srivastava *et al.,* 1989). The modified bulk method of breeding is also by and large quite satisfactory in the improvement of grain yield in wheat.

5.2.4. Inheritance of number of productive tillers per plant

Tillering ability and the fecundity of those tillers are important traits in the attainment of high grain yields in the intensive culture of spring wheat under irrigation. It was thus important to study the inheritance of number of productive tillers and more importantly, the association of this attribute with grain yield and its other component traits. The expression of number of tillers is subject to large environmental and allometric variation as reported by Ketata *et al*.(1976). This was apparent in this study, in which all the generation means including the non segregating generations, were associated with large standard errors.

Unlike the results of Ketata *et al*. (1976) in which the dominant gene effects were small, this study and that of Srivastava *et al.* (1992) in the cross Kalyan Sona x Sonalika, and to a lesser extent, in the cross HD2009 x solanika; dominant gene effects, followed by the additive x additive epistatic gene effects and the additive gene effects, were important in the expression of number of productive tillers per plant. The dominance x dominance epistatic gene action in the two locations in this study and in the cross Kalyan Sona x Sonalika of Srivastava *et al.* (1992) was towards fewer number of tillers, and in the opposite direction to the direction of dominance, thus rendering this epistatic gene action to be of a duplicate or complex type. The additive x additive gene effects showed slight but statistically significant interaction with location, being larger at ORIBI than at ART.

Generation means displayed partial to complete dominance at ORIBI at which the F1 mean was similar to the mid parental value. At this site, both types of heterosis were negative, substantiating the unstable nature of heterotic expression across locations. Broad sense heritabilities were moderate and heritabilities in the narrow sense were low to moderate. Thus the environmental effects were not as pronounced as would be expected in this trait. Large environmental influence on tiller number, makes it difficult to select for this trait at low plant densities as has been reported by Dewey *et al*. (1985). The presence of the small but statistically significant additive and additive x additive components of genetic variation may facilitate genetic improvements through selection in dense stands. The large dominant gene effects and the significant epistatic gene effects would require maintenance of genetic variability in handling the breeding populations until final selection in the advanced homozygous generations.

5.2.5 Inheritance of plant harvest index

Single plant harvest index was in this cross largely governed by additive gene effects as shown in the digenic epistatic models. The dominance gene effects and all the epistatic gene effects were grossly unstable over the two locations, being of opposite direction in the different locations. This was further shown in the significance of the [gh] and the [gl] effects in the non genotype x environment interaction model. Epistatic genetic variation in this cross is of duplicate type, which would complicate early selection for improvement in this trait. Both the additive nature of genetic inheritance and the epistatic gene variation were encountered in harvest index by Batt (1976) in several wheat crosses. Considerable genetic advance may be obtained in selection for harvest index in early segregating generations since the additive genetic component of variation and the heritability in the narrow-sense were large.

5.2.6 Association of single plant traits; plant height, biomass, earmass, number of productive tillers and harvest index

Grain yield of cereals and its related morpho-physiological traits; biomass, number of productive tillers and to a lesser extent, plant height are subject to high environmental variation in sparsely planted culture (Fischer and Kertesz, 1976). Harvest index, being a ratio is expected to be less affected by plant density.

Tall statured wheat genotypes are more prone to allometric compensation than short statured ones. They tiller more readily at wide spacing than the short statured genotypes (Grafius *et al.*, 1976). Thus in this study, the number of productive tillers was positively and significantly (rg = 0,53; P<0.001) phenotypically correlated with plant height. As explained by Sidwell *et al.,* (1976), a higher phenotypic correlation than genetic correlation indicates that environmental effects or additive genetic effects, or both are acting on the two characters in the same direction.

The increase in number of productive tillers per plant phenotypically translated into increased biomass and also earmass per plant as shown by the high positive phenotypic correlations (rp >-0,78; P<0.001) between tiller number and the two traits. The relationships between tiller number and the two yield component traits; biomass and earmass, was also heritable since strong genotypic correlations (rg≥88; P<0.001) were obtained between produvtive tillers and the two traits at both locations. The study of Sidwell *et al.* (1976) in a hard red winter wheat cross, yielded a statistically non significant but moderate genetic correlation between grain yield per plant and tiller number and a strong positive phenotypic correlation (0,68; P<0.01) between them. Kernel weight has been found by Hsu and Watson (1971) and Sidwell *et al.*(1976) to be

strongly negatively genetically correlated with tiller number. Improvement in biomass and grain yield in wheat may therefore not be readily achieved through selection for high tillering ability in spaced plants (Dewey *et al.,* 1985).

Strong and positive genotypic correlations which were associated with moderate but statistically significant positive phenotypic correlations, were obtained between plant height and earmass. Indeed tall statured genotypes within a metre tall, tend to yield, on average, better than very short statured genotypes when they do not lodge in the intensive culture under irrigation in Zimbabwe. Grain yields in excess of ten tonnes per hectare have been achieved with W170/84 and NATA, which are about 95cm tall and are selections from the cross, Kavkaz/buho/kalyansona/Bluebird.

Very strong phenotypic and genotypic corrections (>0,971) were obtained between biomass and earmass of single plants. Similar relationships were also encountered between these two traits when measured in single-ear progenies. Similar to the conclusions of Batt (1977), Jain and Kulshrestha (1976), Rosielle and Frey (1975), Sharma *et al.* (1991) and Sharma *et al.* (1993), high yielding spring wheat genotypes require high biomass for sufficient photosynthesis to fill the grain. Waddington *et al*. (1986) noted that recently developed wheat genotypes in the CIMMYT wheat programme showed higher grain yield and higher biomass yield than the older genotypes, further substantiating the need to maintain high biomass for maximal grain yield expression.

Negative relationship between biomass and HI resulted from increments in biomass that outpaced those in earmass. This result is similar to that of Donald and Hamblin (1976) and that of Sharma (1993). Thus genetic advances in grain yield may not arise from selection for HI alone. As was the case in the study of Sharma (1993), the present findings suggest that some

kind of selection index involving both biomass and harvest index would lead to further improvement in grain yield, since high biomass would be maintained in association with high biological efficiency, arising from high HI.

6 CONCLUSION

The six wheat populations were satisfactorily stratified at the fourth filial generation, into two plant height classes; the short height stratum (≤85cm) and the tall height stratum (≥85cm). The overall plant height mean of accessions in the short height stratum was infact 80,0cm and that of the accessions in the tall height stratum was 94,5cm. The effectiveness of plant height stratification was further substantiated by the small plant height variation which was obtained within plant height strata. Plant height in wheat has been found in this study and in other investigations to be largely under the control of additive gene action. The response to the selection of this character at early stages of segregation, further corroborates this view.

High grain yields (8,6 to10,8 Tones/ha) which were associated with large genotypic variation and non significant variety x site interaction, were expressed in the yield evaluation experiment. This provided an optimum opportunity to compare the relative effectiveness of the different selection criteria in the indirect selection for grain yield among wheat genotypes. Similarity of mean grain yields between the short height and the tall height strata enabled unbiased evaluation of the different selection criteria in the two plant height strata. The high mean grain yields plus the low coefficient of variation obtained in the wheat grain yield evaluation trials at ART and RA indicate that these two locations provide uniform and high yielding environments upon which the grain yield potential of spring wheat genotypes may be assessed in Zimbabwe.

Discrimination of the utilities of single-ear progeny traits; biomass, earmass and HI in the indirect selection of grain yield of wheat genotypes under the intensive irrigated conditions in Zimbabwe, was successfully conducted in this study.

Single-ear progeny earmass was conclusively found to be the best of the three traits in predicting grain yield potential of wheat in the short height stratum (≤85cm) of the six spring wheat populations. Values of the relative selection efficiency which measured the effectiveness of indirect selection over direct selection of grain yield in wheat, were highest (0,95 to1,88) for single-ear progeny earmass in the short height stratum. RSE values were lowest (0,16 to1,03) for single-ear progeny HI and intermediate (0,77 to1,74) for single ear-to-row progeny biomass in the short height stratum of the six wheat populations.

In the short height stratum of the six wheat populations, phenotypic and genotypic correlations which influence the degree of correlated response of grain yield to indirect selection via the three secondary traits, were highest for single-ear progeny earmass (rp = 0,42 to 0,91; $P<0.001$) (rg = 0,66 to 1,40). They were moderate between single-ear progeny biomass (rp = 0,44 to 0,74**) (rg = 0,70 to 1,13). The relationship for single-ear progeny HI and grain yield was inconsistent among the six populations in the short height stratum. Three populations gave moderate correlations (rp= 0,46 to 0,66; $P<0.01$) (rg = 1,44 to 1,98) between the two traits. For the remaining three populations, correlations between single-ear progeny HI and grain yield were low (rp = 0,07 to 0,26) (rg = 0,12 to 0,39) in the short height stratum. Thus single-ear progeny earmass was the most reliable selection criterion for grain yield performance of short statured genotypes.

The application of the three single-ear traits, biomass, earmass and HI, in the indirect selection of grain yield of wheat in in the tall height stratum (>85cm) showed some considerable utility but was not conclusive in the investigation. RSE values were much lower than 1,00 in two out of six populations when single-ear progeny earmass was used as the selection criterion. Single-ear progeny biomass and HI were again the least effective, each giving RSE values much lower than one in three out of the six wheat populations in the tall height stratum.

Since single-ear progeny earmass showed some considerable utility as a selection trait in the tall height stratum of the populations and HI gave high RSE values in three out of the six populations in the tall height stratum, it is suggested that earmass, HI and perhaps biomass of single-ear progenies be used in an index in the indirect selection of grain yield in tall statured wheat genotypes. Earmass and HI reflect both the sink capacity of the wheat genotype and its translocation efficiency. These two traits are likely to improve prediction of grain yield potential among tall statured wheat genotypes. The suggested indices are earmass x HI and earmass x biomass x HI.

Confounding effects of plant height on the effectiveness of the three morpho-physiological traits in the indirect selection of grain yield potential in wheat was evident in this study. Correlations between the responding trait, grain yield and the three single-ear progeny traits; biomass, earmass and HI, were weaker in the unstratified or intact populations than, for instance, in the short height stratum of the six populations. Thus the predictive values in terms of RSEs of single-ear progeny earmass were slightly lower in the unstratified populations (RSE = 0.71, 1.16, 1.20, 1.48, 1.98 and 2.32) than in the short height stratum of the populations (RSE= 0.95, 1.12, 1.23, 1.24, 1.59 and 1.88).

Entry-mean heritability estimates and the corresponding genetic coefficients of variability obtained for single-ear progeny biomass and, in particular, for single-ear progeny earmass, were moderate to high across populations and plant height classes. These were generally higher than the entry-mean heritabilities and G.C.Vs obtained for the responding trait, grain yield, thus raising the scope of indirect selection for grain yield through the selection of favourable phenotypes of the two auxiliary traits. Entry-mean heritabilities and G.C.Vs obtained for grain yield were generally moderate in the unstratified populations and in the short height stratum of

the populations. They were generally low in the tall height stratum of the populations, indicating that genetic variability of grain yield performance was generally low in the tall height stratum of the populations studied. Entry-mean heritabilities and G.C.Vs for single-ear progeny HI were least in magnitude when compared to those obtained for biomass, earmass and grain yield because HI was associated with both high environmental variation and low genotypic variance. Thus the scope of using single-ear progeny HI as an indirect selection trait for grain yield performance was generally lower than that of biomass and earmass. It is however expected to increase in populations with high genetic variability in HI.

The overall effectiveness of indirectly selecting for grain yield of wheat using single-ear progeny earmass was in this study considerable compared to direct selection in replicated yield trials. Since the relationships between grain yield and single-ear progeny earmass were not perfect, the reported degrees of effectiveness discriminate the low yielding wheat genotypes from the rest, but may not be efficient enough to distinguish the best wheat genotypes from the average performing ones. The indirect selection for grain yield using single-ear progeny earmass, however shows promise in the selection of wheat genotypes out of the single-ear progeny generation (usually at F7) into the replicated trial generation. This procedure would increase the frequency of high yielding genotypes which enter into advanced evaluation since the low yielding ones are discarded earlier on. Furthermore the procedure would conserve resources and reduce costs.

The moderate to strong phenotypic (0,38; $P<0.01$ to 0,83; $P<0.001$) and genotypic (0,40; $P<0.01$ to 0,99; $P<0.001$) correlations which were obtained between single ear-to-row progeny biomass and earmass in the unstratified populations and in the short height stratum of the populations in experiment 2, indicate that these two traits strongly positively covary. Single plant biomass was

also strongly correlated with single plant earmass (rp = 0,97; P<0.001 to 0,99; P<0.001) (rg = 0,99; P<0.001 to 1,0; P<0.001) in experiment 3.

Strong correlated response in single-ear progeny biomass is expected when single-ear progeny earmass is under selection. Their relationship however tends to weaken with increase in plant stature. This partly explains the negative relationship which was encountered between biomass and HI of single-ear progenies in the tall height stratum. Harvest index of single-ear progenies was consistently positively correlated with earmass across the plant height classes (rp = 0,24; P<0.05 to 0,81; P<0.001) (rg = 0,30; P<0.05 to 0,96; P<0.001). Thus the increments in biomass outpaced those in earmass for the relationship between biomass and HI to be negative.

While the correlation between single-ear progeny HI and plant height was found to be weak and negative, those between single-ear progeny ear traits, plant height and earmass and plant height and biomass were strong and positive because tall plants yield more phytomass and bear larger panicles in spaced plantings than short statured ones. The strong relationships of some of the selection traits with plant height necessitated the stratification of the populations into uniform plant stature in the indirect selection for grain yield of wheat.

In the study of inheritance of important traits in experiment 3, plant height was found to be under the control of large additive gene action. This was also reflected in the relatively high narrow sense heritabilities for the trait. Plant height can thus be effectively selected during early stages of segregating generations. Additive and additive x additive epistatic gene effects seemed important in the control of harvest index. The remaining three traits; single plant biomass, earmass and productive tillers were under large dominant gene effects and were also associated with large additive x additive and large additive x dominant epistatic gene effects, which were

environmentally unstable. The apparent lack of stability of dominance and epistatic gene effects invoke the need for environment specific inheritance studies. Breeding methods which maintain high genetic variability until final selection in the homozygous generations would be more appropriate in the improvement of the four traits.

The following recommendations and suggestions were made from this study:

1. Stratification of semi advanced wheat populations (at about the fourth filial generation) into uniform plant height classes, has merit in the use of single-ear progeny traits for indirect selection for grain yield ability of irrigated wheat in Zimbabwe.
2. Single-ear progeny earmass can satisfactorily predict grain yield performance of irrigated spring wheat and thus may be used to upgrade advanced wheat lines into replicated yield evaluation.
3. Selection indexes involving single-ear progeny earmass and single-ear progeny HI, and probably single-ear progeny biomass in the form of earmass x HI and earmass x biomass x HI seem justified in the selection of tall statured wheat genotypes but these selection criteria require to be evaluated for firm recommendation to be made.
4. Further inheritance studies of grain yield, biomass, earmass and HI of wheat over several locations in Zimbabwe are suggested in order to fully ascertain the magnitude of *gei* on genetic effects.
5. Genetic improvement of grain yield, biomass, earmass, HI and production of fertile tillers appears complex and thus requires intermating, followed by maintenance of genetic variability until final selection in homozygous generations.