STUDIES ON GENOTYPIC VARIABILITY AND INHERITANCE OF WATERLOGGING TOLERANCE IN WHEAT

By

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DECLARATION

I hereby declare that this dissertation, prepared for the degree Philosophiae Doctor, which was submitted by me to the University of the Free State, is my own original work and has not previously in its entirety or in part been submitted to any other university. All sources of materials and financial assistance used for the study have been dully acknowledged. I also agree that the University of the Free State has the sole right to the publication of this dissertation.

Signed on 13th of March 2001 at the University of the Free State, Bloemfontein, South Africa.

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This work is dedicated to:

- *my wife Sebash Kassahun;*
- *our children: Sinkie, Mastewal and H/Michael*
- *and to my parents: Fetenech Alene and Tarekegne Tesfaye*

"And he gave it for his opinion, that whoever could make two ears of corn or two blades of grass to grow upon a spot of ground where only one grew before, would deserve better of mankind, and do more essential service to his country than the whole race of politicians put together".

JONATHAN SWIFT (1667-1743)

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ABBREVIATIONS

CIMMYT	=	International Maize and Wheat Improvement Center
CIMMYT/CIDA	=	International Maize and Wheat Improvement Center / Canadian International Development Agency
CIMMYT/EU	=	International Maize and Wheat Improvement Center / European Union
GD	=	Genetic distance
COP	=	Coefficients of parentage
MRD	=	Modified Roger's distance
GD-SSP	=	Genetic distance based on seed storage protein
WCOP	=	Wheat Coefficient of Parentage
IWIS	=	International Wheat Information Sysytem
MANOVA	=	Multiple Analysis of Variance
ANOVA	=	Analysis of variance
CV	=	Coefficients of variations
SAS	=	Statistical Analysis System
CWl	=	Continuous soil waterlogging
TWl	=	Transient soil waterlogging
FD	=	Free drainage
AUCPC-value	=	Area Under Chlorosis Progress Curve value
BYm	=	Above ground (soil surface) dry biomass yield at maturity ($g\ pot^{-1}$)
BYv	=	Biomass yield (vegetative) at the end of treatment;
Chl	=	Chlorosis
ESP	=	Exchangeable sodium percentage
DPH	=	Days to physiological maturity;
DH	=	Days to heading;
GLN	=	Green leaf numbers per four main plants.
TLN	=	Total leaf number per four main stems
TNG	=	Total Grains per pot (no)

GPms	=	Grains per main spike
GPts	=	Grain per tiller spike
GPSa	=	Grains per spike (average)
GPSl	=	Grains per spikelet (no.)
GYt	=	Total grain yield per pot
GYms	=	Grain yield of all main spikes in a pot (g pot^{-1})
GYts	=	Grain yield of all tiller spikes in a pot (g pot^{-1})
KM	=	Kernel mass (mg $kernel^{-1}$:)
PHm	=	Plant height at maturity (cm)
PHv	=	Plant Height (vegetative) at the end of treatment (cm)
PHs	=	Plant Height (seedling) at the start of treatment (cm)
PS	=	Productive spikes per pot
SER	=	Seedling shoot elongation rate (cm day^{-1})
SL	=	Spike length (cm)
SlPS	=	Spikelets per spike (no.)
SSI	=	Stress susceptibility index
STI	=	Stress tolerance index
WK	=	Week
APS	=	Ammonium persulphate.
HMW-GS	=	High molecular weight glutenin subunits
LMW-GS	=	Low molecular weight glutenin subunit
SDS	=	Sodium dodecyle sulphate
SDS-PAGE	=	Sodium dodecyl sulphate-polyacrylamide gel electrophoresis
SDS-PAGE	=	Sodium dodecyl sulfate-polyacrylamide gel electrophoresis
TEMED	=	N, N, N^1, N^1-tetramethylethylenediamine

w/v	=	weight per volume
w/w	=	weight per weight
µg	=	microgram
µl	=	micro liter
rpm	=	revolutions per minute
mm	=	millimeter
ml	=	milliliter
mg	=	milligram
mA	=	milliamp ere
hr	=	hour
g	=	gram
°C	=	degrees Celsius

CHAPTER I

INTRODUCTION

Wheat (*Triticum* ssp.), like any other mesophyts, requires an environment, which is neither too dry nor too wet for maximum growth and productivity. Most of the worlds' wheat, however, is grown in marginal agro-climatic zones, where yield is often affected by drought or excess moisture (Briggle and Curtis 1987).

Waterlogging is a soil condition whereby excess water in the root zone inhibits gas exchange with the atmosphere above the soil surface (Setter and Belford, 1990). Waterlogging of soils can be temporary, intermittent (transient), or continuous ponding of excess surface water on the agricultural fields. The excess water can arise from flood irrigation (Meyer *et al.*, 1985; Melhuish et al., 1991; MacEwan *et al.*, 1992), seepage from irrigation cannels (Reid, 1977), development of a perched water table (Grieve *et al.*, 1986; MacEwan *et al.*, 1992; Gardner and Flood, 1993), or high rainfall in areas characterized by level topography and high clay soils (Cannell *et al.*, 1980; Van Ginkel *et al.*, 1992; Musgrave and Ding, 1998).

Waterlogging of soils occurs over vast regions throughout the world (Kozlowski, 1984; Krizek, 1982; Armstrong, 1982). Donman and Housten (1967) estimated that about 30 to 50% of the worlds' irrigated arable land has drainage problems. Lal (2000) estimated that about 15% of rainfed agriculture in sub-Saharan Africa and a total of 20% in developing countries has soil waterlogging problems. Waterlogging of soils affects about 2.5 million hectares of land in the irrigated Indo-Gangetic alluvial plains of Northern India (Sharma and Swarup, 1988, 1989). About 15.7% of agricultural soils in the U.S.A. are affected by soil waterlogging (Boyer, 1982). In Great Britain, 40% of the cereal growing areas have waterlogging problems. About 3.75 million hectares of land in Victoria, Australia, have waterlogging problems (MacEwan *et al.*, 1992). In Western Canada, 24,000 of the 280,000 hectares of irrigated land are permanently waterlogged due to seepage water from cannels

(Reid, 1977). An estimated 10-15 million hectares of wheat in the developing world experience moderate to serious waterlogging problems (Sayre *et al.*, 1994; Villareal and Mujeeb-Kazi, 1999).

Heavy clay soils, such as Vertisols appear to be more prone to waterlogging stress than light soils (Cannell *et al.*, 1980; Grieve *et al.*, 1986; McDonald and Gardner, 1987; Meyer *et al.*, 1985). Vertisols are agriculturally important soil groups in many parts of the world (Coulombe *et al.*, 1996); they are estimated to compose about 308 million hectares (2.23%) of the earth's surface (USDA-SCS, 1994), and 90% of these soils are found in tropical and sub-tropical regions (Coulombe *et al.*, 1996). In high rainfall areas such as in the central and eastern African highlands, the duration and severity of waterlogging stress are highly pronounced due to widespread occurrence of Vertisols (Debele, 1985; Jutzi and Abebe, 1986) and low evaporative demand (Simane *et al.*, 1999) during crop growing seasons. In the Ethiopian highlands alone, Vertisols cover about 8 million hectares, of which only 24% is currently under cultivation (Debele, 1985; Jutzi and Abebe, 1986). In these regions, therefore, croplands become affected by extreme waterlogging stress early in the rainy season and remain waterlogged for about 50% of the growing season (late June to early September).

The principal effect of soil waterlogging on plant growth is the restriction of O_2 availability to the roots (Armstrong, 1982, 1992; Trought and Drew, 1982; Drew, 1983; Cannell *et al.*, 1984; Belford *et al.*, 1985; Box, 1986; Setter and Belford, 1990). Soil oxygen deficiency can restrict plant performance directly through impaired root metabolism such as retarded respiration, hormonal imbalance and membrane impermeability (Huang and Johnson, 1995; Huang *et al.*, 1997; Thomson *et al.*, 1990; Voesenek and van der Veen, 1994), or indirectly by altering plant nutrient availability in the soil solution (Trought and Drew, 1980b; Sharma and Swarup, 1988, 1989; Meyer *et al.*, 1985; Stepniewski and Przywara, 1992; Huang *et al.*, 1995) and making certain compounds to accumulate in the soil to phytotoxic levels (Pannamperuma, 1984). Excess soil moisture, therefore, adversely affects seed germination and emergence, restricts root growth and impairs uptake of nutrients,

accelerates premature leaf senescence and drying, slows down rates of leaf emergence and dry matter accumulation, restricts tillering and grain setting and weight, delays maturation, and finally depresses grain yields (Watson *et al.*, 1976; Cannell *et al.*, 1980, 1984; Trought and Drew, 1980a, b; Belford, 1981; Sharma and Swarup, 1988, 1989; Davies and Hillman, 1988; Thomson *et al.*, 1992; Gill *et al.*, 1993; Huang *et al.*, 1994a, b; Cai *et al.*, 1994b; Musgrave and Ding, 1998). Waterlogging has been reported to reduce wheat grain yield by up to 73% (Luxmoore *et al.*, 1973), which may partly be attributed to genotypic differences (Davies and Hillman, 1988; Huang *et al.*, 1994a, b; Cai *et al.*, 1994b; Van Ginkel *et al.*, 1992; Musgrave and Ding, 1998). In Ethiopia, up to 100% yield losses has been observed in wheat due to prolonged waterlogging on the highland Vertisols (Belayneh, 1986; Bechere *et al.*, 1994).

Productivity of wheat on soil susceptible to waterlogging stress may be improved by introducing efficient field drainage systems (Jutzi and Abebe, 1986; Belayneh, 1986; Gebre, 1988; MacEwan *et al.*, 1992). On the highland Vertisols in Ethiopia, improved drainage of excess surface water using permanent camber beds or temporary broad-beds and furrows have increased grain yields of wheat by 130% over the undrained control (Belayneh, 1986; Jutzi and Abebe, 1986). Furthermore, improved drainage has made early planting possible and increased nutrient use efficiency (Belayneh, 1986; Gebre, 1988). Such management options, however, are often inadequate under prolonged waterlogging conditions and construction of drainage systems may not always be possible, as the required drainage system my sometimes be impractical. The economic viability of drainage systems may also be questionable, as they require a large investment for implementation of the system (Gebre, 1988; Villareal and Mujeeb-Kazi, 1999). The waterlogging problem can, therefore, be partly addressed through development of genotypes with increased ability to withstand temporary or prolonged waterlogging stress conditions (Villareal and Mujeeb-Kazi, 1999; Van Ginkel *et al.*, 1992). Genotypic variability for waterlogging tolerance has been reported in several agricultural crop species, including wheat (Davies and Hillman, 1988; Thomson *et al.*, 1992; Van Ginkel *et al.*, 1992; Boru, 1996; Cai *et al.*, 1994a; Cao *et al.*, 1995; Cao and Cai, 1991, Taeb *et al.*, 1993). Wheat in the highlands of Ethiopia is

prone to prolonged waterlogging stress and hence breeding for tolerance is a major objective to improve the productivity of wheat.

Genetic diversity in the available gene pool is the foundation of all plant improvement programs because it is a source of variation which is a raw material for the improvement work, and is essential to decrease crop vulnerability to abiotic and biotic stresses, ensure long-term selection gain in genetic improvement, and promote rationale use of genetic resources (Martin *et al.*, 1991; Barrett and Kidwell, 1998; Messmer *et al.*, 1993; Tesemma *et al.*, 1991). In Ethiopia, bread wheat (*Triticum aestivum* L) is believed to be a relatively recent introduction into an old tradition of durum wheat (*T. durum* Desf) culture. Although bread wheat exhibits wider adaptation and higher yield potential than the indigenous durum wheat (Gebre-Mariam, 1991; Tarekegne *et al.*, 1995a, b), its genetic variability is generally believed to be limited (Gebre-Mariam, 1991). Hence, assessment of genetic diversity in the adapted bread wheat genotypes would facilitate development of cultivars for the specific production constraints by providing an index for parental selection, structure for stratified sampling and predictive measures of genetic variances and heterotic responses.

The general objectives of the study were:

1. To assess genetic diversity of Ethiopian-grown bread wheat cultivars and lines based on their seed storage protein composition.
2. To assess genotypic variability for tolerance to prolonged waterlogging stress and identify plant characters associated with tolerance.
3. To determine the effects of waterlogging on mineral nutrient uptake of selected wheat genotypes and assess changes in soil chemical and mineral nutrient status.
4. To study the nature of inheritance of waterlogging tolerance and heterosis in a diallel cross of selected tolerant and susceptible parents under waterlogged and drained environments.

CHAPTER II

LITERATURE REVIEW

2.1. Genetic Diversity and Cultivar Relationships

2.1.1. Wheat Production in Ethiopia:

Wheat (*Triticum* ssp.) is historically one of the principal traditional cereal crops grown in the highlands of Ethiopia. It is the fifth most important cereal crop both in terms of area and production after tef (*Eragrostis tef*), maize (*Zea mays*), barley (*Hordium vulgare*) and sorghum (*Sorghum bicolour*) (CSA, 1997). Ethiopia is the second largest wheat producer in Sub-Saharan Africa with an annual production of about 1.2 million tons of bread and durum wheats on about 0.85 million hectares (Gebre-Mariam, 1991).

In Ethiopia, wheat grows in the highlands between 6° and 15° N latitude and 37° and 42° E longitude, at altitudes ranging from 1500 to 3400 m a.s.l (Gebre-Mariam, 1991). At present, wheat is produced solely under rainfed conditions. The rainfall distribution is bimodal and ranges between 600 and 2000 mm per annum (Simane *et al.*, 1999). The rainy season is divided into the short rains ("belg") falling from February to April and the main rains ("meher") falling from June to September. This allows farmers to grow two crops in a year in some parts of the country. The climate is temperate with the maximum and minimum temperatures ranging from 25 to 30 °C, and from 3 to 8 °C, respectively. Wheat grows across a wide range of soil conditions in Ethiopia; however, poorly drained heavy black clay soils (Vertisols) are the most important soil groups used for wheat production (Gebre-Mariam, 1991; Tesemma and Belay, 1991; Tarekegne *et al.*, 1999).

Ethiopia, with its range of altitudes, soils and climatic conditions, provides ecological settings suitable for the cultivation of diverse species of wheat (Harlan, 1971, 1975). Durum wheat (*Triticum durum* Desf) and bread wheat (*T. aestivum* L. em. Thell) are, however, the two most important wheat species grown in the country although other species are also cultivated, but to a lesser extent. Bread wheat is believed to be a relatively recent introduction to Ethiopia

(Gebre-Mariam, 1991); it exhibits wider adaptation and higher yield-potential than durum wheat (Tarekegne *et al.*, 1995a, b). Waterlogging of soils, particularly on highland Vertisol, which covers about 8 million hectares of arable land in the highland (Debele, 1985), has been demonstrated to be one of the principal constraints for wheat production (Tarekegne *et al.*, 1999).

2.1.2 Genetic diversity:

Genetic diversity is the foundation of all plant improvement programs. It is a measure of individual variation within population and reflects the frequency of different types in the population (Gregorius, 1987). Diversity is derived from the wild progenitors, modified in response to cultivation and hence, it is a function of ancestry, geographic separation and adaptation to differing environments (Moll *et al.*, 1965). Within a given plant population, diversity is a product of an interplay of biotic factors, physical environment, artificial selection and plant characters such as size, mating system, mutation, migration and dispersal (Frankel *et al.*, 1995). Harlan (1975) attributed the accumulation of genetic variation in the centers of diversity to artificial selection, environmental factors and the dynamics of hybridization with the subsequent segregation and selection. Genetic diversity in domesticated crop species provides a source of variation which is a raw material for the improvement of agricultural crops, and is essential to decrease crop vulnerability to abiotic and biotic stresses and to ensure long-term selection gain in genetic improvement and to promote rationale use of genetic resources (Martin *et al.*, 1991; Barrett and Kidwell, 1998; Messmer *et al.*, 1993; Smith and Smith, 1989).

Progress in plant breeding could be enhanced through a more complete knowledge of germplasm contribution and a thorough understanding of genetic relationships between genotypes in a given gene pool. Information about genetic diversity in the available germplasm is important for the optimal design of breeding programs. Therefore, the notion of genetic relationships among lines, populations or species has become an important tool for the

effective management of genetic diversity in a given gene pool (Manjarrez-Sandoval *et al.*, 1997). Genetic distance estimates have been proven to be useful in many autogamous crop species including wheat to: i) examine the level of genetic diversity (effective population size) of a given germplasm pool (Murphy *et al.*, 1986; Souza and Sorrells, 1991 a and b; Van Beuningen and Buscha, b); ii) to monitor trends in germplasm usage (Cox *et al.*, 1986; Messmer *et al.*, 1992; 1993); iii) to identify major groupings of related cultivars, breeding materials, and genetic resources (Messmer *et al.*, 1993; Graner *et al.*, 1994); iv) to select parents for establishing new base populations (Bohn *et al.*, 1999; Graner *et al.*, 1994; Manjarrez-Sandoval *et al.*, 1997); v) for rational utilization of genetic resources (Graner *et al.*, 1994). In Ethiopia, genetic diversity within and between landrace populations of tetraploid wheat has been studied based on highly heritable morphological characteristics (Srivastava *et al.*, 1988; Tesemma *et al.*, 1991; Tesemma and Belay, 1991; Bechere *et al.*, 1996), isozyme data (Tsegaye *et al.*, 1994), and on DNA-based RFLP marker data (Autrique *et al.*, 1996). The level and distribution of genetic diversity as well as genetic relationships among adapted modern cultivars of bread wheat, however, have not been studied in Ethiopia.

2.1.3. Measures of genetic distance:

The pattern and the level of genetic diversity in a given crop gene pool can be measured in terms of genetic distances. Genetic distances are measures of the average genetic divergence between cultivars or populations (Souza and Sorrells, 1991b). Moll *et al.* (1965) defined genetic divergence of two varieties as a function of their ancestry, geographic separation, and adaptation at differing environments. Genetic distance is the extent of gene differences between cultivars, as measured by allele frequencies at a sample of loci (Nei, 1987). Genetic similarity is the converse of genetic distances, i.e., the extent of gene similarities among cultivars. The measure of distance or similarity among cultivars is the covariance of allele frequencies summed for all characters (Smith, 1984).

Measures of genetic proximity or relationship can be derived from genetic marker data and coefficients of parentage (COP). Several genetic distance measures have been used to quantify genetic relationships among cultivars or germplasm accessions. Each variable of molecular marker bands such as isozyme, storage proteins and DNA-based marker bands are considered a locus so that every locus has two alleles. Banding profiles of each line or cultivar can be scored as present (1) or absent (0). Pairwise binary matrices are constructed from the arrays of 1s and 0s to calculate genetic distances based on a range of formulae. One of the most useful genetic distance formulae is that of Euclidean distance, which is the square root of the sum of squares of the distances between the multidimensional space values of the distances for any two cultivars (Kaufman and Rousseeuw, 1990) and is written as: $GD = \sqrt{\sum[(X_I - Y_I)^2 / N]}$, where *GD* is the genetic distance between individual X and individual *Y*; $i = 1$ to *N*; *N* is the total number of bands, and X_i and Y_i are i^{th} band scores (1 or 0) for individual *Xs* and *Ys*. The other genetic distance measures include Manhattan distance (Kaufman and Rousseeuw, 1990) and Roger's distance or Modified Roger's distance (*MRD*) (Rogers, 1972). Genetic distance has been also generated from several genetic similarity indices (*GS*), which can be calculated as *1-GS*. One use full similarity index is that of Nei and Li (1979): $CD = 1 - [2N_{XY} / (N_X + N_Y)]$, where $2n_{xy}$ is the number of shared bands, and the *nx* and *Ny* are the number of bands observed in individual *x* and individual *y*, respectively. Other similarity indices such as Jaccard's (Rohlf, 1993) and Gower's similarity coefficients (Gower, 1971) have been extensively used in genetic distance determination (Barrett and Kidwell, 1998; Yee *et al.*, 1999; Barrett *et al.*, 1998). Genetic distances have also been determined from coefficients of parentage (*COP*) obtained from cultivar pedigree documents (Cox *et al.*, 1985a; Cox *et al.*, 1986; Murphy *et al.*, 1986; Graner *et al.*, 1994; Kim and Ward, 1997; van Beuningen and Bush, 1997 a and b; Barrett *et al.*, 1998), as *1-COP* Kempthorne, 1969). The *COP* is the covariance of allele frequencies between cultivars as determined by identity of parentage (Cox *et al.*, 1985a).

The pattern of genetic relationship or proximity among cultivars can be conveniently shown by multivariate techniques such as cluster analysis or ordination analysis. Clustering techniques can present complex, multidimensional patterns of diversity (Sneller, 1994). Clustering is a useful tool for studying the relationships among closely related cultivars or accessions. In cluster analysis, cultivars or lines are arranged in hierarchy by agglomerative algorithm according to the structure of a complex pair wise genetic proximity measures. The hierarchies emerging from cluster analysis are highly dependent on the proximity measures and clustering algorithm used (Kaufman and Rousseeuw, 1990; Hintze, 1998). Five different clustering algorithms are available in NCSS 2000 computer package for cluster analyses (Hintze, 1998): i) Single linkage, ii) the average linkage method called Unweighted Pair Group Method using Arithmetic Average (UPGMA), iii) the average linkage method called Unweighted pair Group Method using Centroids (UPGMC), iv) Complete Linkage, and v) Ward's method. Clustering technique, however, cannot provide an insight into the underlying causes of patterns in genetic diversity.

In ordination techniques, the multidimensional variability in a pairwise, inter marker proximity is depicted in one to several dimensions through eigen structure analysis. It permits the presentation of the clusters as points in Euclidean space (Murphy *et al.*, 1986). Ordination is best suited to revealing interactions and associations among cultivars or germplasm accessions which are described by continuous quantitative data (Brettings and Widrlechner, 1995). Principal component, principal coordinate, and linear discriminate analyses are the ordination techniques most frequently used in genetic relationships and cultivar classification studies (Murphy *et al.*, 1986; Sneller, 1994; Schut *et al.*, 1997). Sneller (1994) has, however, indicated that the distances and patterns inferred from two dimensions can have limited validity if they do not account for a large proportion of the total variance in the data set.

2.1.4. Data sources for genetic distance analyses:

Knowledge about genetic relationships among cultivars is usually obtained indirectly from eco-geographic information about the genotypes, pedigree and heterosis data, and directly from plant characteristic data such as morphological traits, biochemical data, and more recently, on DNA based marker data (Schut *et al.*, 1997).

Pedigree identity: Parentage analysis, when pedigree records are available, is the most widely used and least expensive indirect measure of genetic diversity and genetic relationship among cultivars in various autogamous crops (Souza and Sorrells, 1989; Cox *et al*, 1985a, b, 1986; Murphy *et al.*, 1986; Martin *et al.*, 1991; Sneller, 1994; van Beuningen and Busch, 1997a). Pedigrees of the varieties and lines are often traced back to landraces and wild accessions. Coefficients of parentage (COP) summarize genealogical information from an array of cultivars. Originally devised by Wright in 1922 and Melecot in 1948 (see Souza and Sorrells, 1989 for review), the COP between two cultivars is defined as the probability that a random allele taken from a random locus in one cultivar is identical by descent to a random allele present at that same locus in the second cultivar (Kempthorne, 1969; Cox *et al.*, 1985a). With this context, COP can be used as an index of genetic relationship among cultivars, with values ranging from 0, where two cultivars are completely unrelated and hence no alleles in common, to 1, where two cultivars share all alleles in common. COP analysis has been applied in several crop species including soybean (Cox *et al.*, 1985a; Sneller, 1994), wheat (Cox *et al.*, 1985b, 1986; Murphy *et al.*, 1986; van Beuningen and Busch, 1997a, c), barley (Martin *et al.*, 1991), and oat (Souza and Sorrells, 1989). Murphy *et al.* (1986) surveyed the U.S. winter wheat pedigree and observed that soft red and hard red winter wheat cultivars formed two separate gene pools with some overlapping to produce an in-between group germplasm. Cox *et al.* (1986) monitored the change of genetic diversity of these two gene pools using COP values weighted by the acreage data of cultivars in a given year. The genetic relatedness of the U.S. soft red winter wheat gene pool has not changed remarkably when measured by acreage-weighted COP (i.e., from 0.30 in 1919 to 0.22 in 1984). On the other

hand, mean acreage–weighted COP within the hard red winter wheat gene pool has significantly declined from 1.0 to 0.4 in the same period. In similar analysis of oat pedigree, Souza and Sorrells (1989) concluded that oat gene pool in U.S. is expanding over time.

Accuracy of COP analysis depends on the availability of reliable and detailed pedigree records for all cultivars in the study. Pedigree data, however, are not always obtainable or correct. For instance, pedigree records from some remote ancestors are either incomplete or names of cultivars are ambiguous. For modern cultivars, pedigrees are increasingly becoming complex because un-adapted and wild germplasm sources from diverse geographic regions have been introgressed into elite wheat germplasm for new resistance genes to fungal and viral diseases, but their true genetic contributions are unknown. Also, private breeding companies have protected pedigrees of the modern cultivars as trade secret. Under these conditions, calculation of COP is often not feasible or is dubious (Graner *et al.*, 1994; Melchinger *et al.*, 1991, 1994). Furthermore, estimates of relationships based on COP might be incorrect because of inadequate simplifications in the understanding the model that assumes no relation amongst original ancestors of the relevant gene pool, equal parental contributions, no selection pressure, no mutation and no random genetic drift (Martin *et al.*, 1991; Melchinger *et al.*, 1994; Barrett *et al.*, 1998; Messmer *et al.*, 1993; Murphy *et al.*, 1986; Cox *et al.*, 1985 a and b).

Heterosis data: Heterosis in the F_1 progeny has been used as an indicator of genetic diversity between parents. Assuming that heterosis is a function of heterozygosity, heterosis should be an increasing function of parental diversity (Smith and Smith, 1989; Martin *et al.*, 1995). A heterotic group is a collection of closely related inbred lines. The co-ancestries within a heterotic group are usually high, whereas the co ancestries between two heterotic groups comprising a heterotic pattern are usually low. These data are presumed to survey numerous loci that are widely spread throughout the genome; the precise locations and magnitudinal effects of those loci are, as yet, unknown. They have shown relationships between lines that

closely mirror those to be expected on the basis of unknown pedigree (Smith and Smith, 1989). For these reasons, heterosis is generally considered to be an indicator of genetic relationships, at least across a relatively limited range of germplasm as would usually be the case with elite breeding materials (Moll *et al.*, 1965).

Morphological data: Traditionally, genetic similarity estimates in agricultural crop species were based on differences in morphological characters and quantitative traits (Schut *et al.*, 1997; Goodman, 1972). Typically, genotypes are grown in the field or greenhouse, and estimates of relationships are based on the range of expression of various traits among genotypes. When phenotypic estimates are used to represent the degree of genetic relationship between two lines or populations, it is assumed that similarity in phenotype accurately reflects similarity in genotype (Cox *et al.*, 1985b; van Beuningen and Bush, 1997b). This approach has been extensively used in genetic similarity and diversity studies (Souza and Sorrells, 1991a; van Beuningen and Bush, 1997b; Tesemma *et al.*, 1991; Bechere *et al.*, 1996). Morphological traits continue to be the first useful step in the studies of genetic relationships in most breeding programs because: i) the existing data bases on the germplasm collection or breeding stocks can often be used for genetic analysis; ii) statistical procedures for morphological trait analysis are readily available; iii) morphological information is essential in understanding the ideotype-performance relationships; and iv) explanations of heterosis may be enhanced if morphological measures of distance are included as an independent variable (Cox and Murphy, 1990; van Beuningen and Busch, 1997b).

However, use of morphological traits for the study of genetic relationship has been criticized. Genetic relationship evaluation among germplasm using morphological characteristics are lengthy and costly processes (Cooke, 1984). The genetic control of many morphological characters is assumed to be complex, often involving epistatic interactions, and has often not been elucidated (Smith and Smith, 1989). Many morphological markers are recessive and therefore only expressed in the homologous condition. Most elite cultivated and breeding

materials do not abound with an array of readily observable morphological markers, a large number of which have deleterious effects on agronomic performance (Smith, 1986). Furthermore, most morphological attributes are subject to large genotype x environment interaction effects (Yee *et al.*, 1999). Hence, morphological appearance cannot adequately describe cultivars without extensive replicated trials and, therefore, valid comparisons are only possible for descriptions taken at the same location during the same season (Smith and Smith, 1989).

Biochemical data:

Isozymes: Direct measures of genetic similarity between individuals have been determined from isozyme markers in many crop plants (Brown, 1979). Isozymes are variants of the same enzyme having identical or similar function, but differing in electrophoretic mobility. They reveal differences in the gene sequence and function as co-dominant markers (see Kumar, 1999 for review). Isozyme data can be used to quantify similarities and differences between genotypes because: i) isozyme surveys represent a basic level of investigation for species that are poorly documented; ii) isozymes are universal in a sense that estimates of the extent of distribution of genetic diversity can be directly compared between individuals, populations, or species; and iii) isozyme methods are appropriate to investigate genetic variation from large samples of individuals because the procedure is fairly quick, simple and inexpensive, and interpretation is relatively easy (Cooke, 1984). Nevertheless, enzyme-encoding loci do not constitute a random sample of genes, and they are not randomly dispersed through the genome. Some isozyme variants are not selectively natural and electrophoresis will detect only a portion of the actual variability present in amino acid sequence (see Brettings and Widrechner, 1995 for review). Hence, isozyme data, although they provide new insights into genetic relatedness among elite breeding materials, their usefulness for obtaining reliable estimates is generally limited by the insufficient sampling of the genome (Melchinger *et al.*, 1991), small number of loci and low degree of polymorphism among closely related genotypes (Messmer *et al.*, 1992). Furthermore, isozyme expression can be significantly

influenced by the environmental factors and management practices and by plant development stage (Bellamy *et al.*, 1996; Beeching *et al.*, 1993).

Seed storage proteins: The endosperm proteins of wheat grain consist predominantly of two classes of storage proteins termed gliadin and glutenin (Wall, 1979). Gliadins are monomeric proteins consist of a complex mixtures of single polypeptide chains, associated by hydrogen bonds and hydrophobic interactions (Shewry and Tatham, 1990). They are a highly heterogeneous group of proteins with molecular weight ranging from 20 to 70 KDa (Southan and MacRitchie, 1999) and, when fractionated by gel electrophoresis at low pH, separate into α-, β-, γ-, and ω-gliadins (Woychik *et al.*, 1961). Glutenins, on the other hand, are aggregates of polypeptides (polymers) that are cross-linked mainly by covalent disulphide bonds (Wall, 1979; Wrigley, 1982); they have been shown to include subunits of the high molecular weight (HMW-GS) (Payne *et al.*, 1981), with a molecular mass ranging from 80 to 120 KDa (Southan and MacRitchie, 1999) and the low molecular weight (LMW-GS) (Jackson *et al.*, 1983) with a molecular mass ranging from 30 to 55 Kda (Southan and MacRitchie, 1999).

The endosperm of the wheat grain usually contains between 7 and 15% of protein by weight, of which 85% are storage proteins. Gliadins account for about 50% of the total storage proteins, where as HMW-GS and LMW-GS share the remaining 10 and 40%, respectively (Payne, 1987).

The chromosomal location of structural genes encoding for storage proteins in hexaploid wheat has been reported by Payne (1987). The genes encoding the storage proteins are located at nine major loci on the homoeologous chromosome groups 1 and 6 of bread wheat. The HMW subunits are encoded by genes at three loci designated as *Glu-A1*, *Glu-B1* and *Glu-D1*, which occur on each of the long arms of chromosomes 1A, 1B and 1D, respectively (Wrigley, 1982; Payne, 1987). The LMW subunits are encoded by genes at the loci designated as *Glu-A3*, *Glu-B3* and *Glu-D3* on the short arms of the same chromosomes (Singh and Shepherd,

1988; Jackson *et al.*, 1983). Gliadins are coded by genes at *Gli-1* (*Gli-A1*, *Gli-B1* and *Gli-D1*) and *Gli-2* (*Gli-A2*, *Gli-B2* and *Gli-D2*) loci located on the distal parts of the short arms of both group 1 (associated with *Glu-3*) and group 6 chromosomes (Metakovsky, 1991). Durum wheat with the AABB genome constituent lacks the D-genome and hence the *Glu-D1*, *Glu-D3*, *Gli-D1* and *Gli-D2* loci are present only in bread wheat (with genome AABBDD).

Variation in the storage protein composition of wheat cultivars has been associated with the presence of allelic genes tightly linked as clusters at each of these nine complex loci (Galili and Feldman, 1983; Payne *et al.*, 1981). Both gliadins and glutenins have demonstrated extensive multiple allelism at their encoding genes and hence storage proteins are highly polymorphic (Metakovsky, 1991; Payne *et al.*, 1981). From several to more than 30 alleles were identified from each of the six major gliadin-encoding loci (three *Gli-1* and three *Gli-2*) (Metakovsky, 1991) and for the major glutenin coding loci, *Glu-1* and *Glu-3* (Payne and Lawrence, 1983; Gupta and Shepherd, 1988). Konarev and his co-workers (1979) have suggested that polymorphism in protein components may result from gene mutations, or from quaternary structure composed of associated subunits, or secondary modifications of proteins by amidation, deamidation, acetylation, and phosphorelation of amino acid side chains. Levy and co-workers (1988) also indicated that at the gene cluster levels, polymorphism stems from: a) the number of active genes within a gene cluster; b) the number of alleles of each active gene; c) the combination of the different alleles of active genes of the same genome, resulting in different band patterns; and d) the combination of different genomic patterns.

Polymorphism of storage proteins, as manifested in a variety of molecular forms, is evident from various types of electrophoretic techniques that detect charge and size differences (Konarev *et al.*, 1979; Bushuk and Zillman, 1978). The various types of electrophoretic methods available for protein analysis includes one –dimensional starch gel electrophoresis, polyacrylamide gel electrophoresis (PAGE: with or without sodium dodecyl sulfate: SDS), iso-electrophoresis (IEF), and two-dimensional polyacrylamide gel electrophoresis (Wrigley,

1992; Cooke, 1984). Polyacrylamide gel electrophoresis in the presence of SDS has been used world wide for the analysis of wheat seed storage proteins (Wrigley, 1992; Galili and Feldman, 1983). This technique is rapid, relatively low cost, and capable to handle a large number of samples (Gept, 1990). It enables a detailed study of the number, size, distribution and the genetic control of specific protein at the subunit or block levels (Galili and Feldman, 1983).

Seed storage proteins, because they are the primary products of structural genes, which, in turn, are coupled into genetic systems, can serve as markers for the genes that encoded them and the system they are located in, which may be a set of genes, chromosome or genome as a whole (Cooke, 1984; Wrigley, 1982; Konarev *et al.*, 1979). The composition of proteins, therefore, reliably reflects the underlying variation in genetic expression of an individual and its relationship with its progenitors. As genetic markers, seed storage proteins are characterized by a high level of polymorphism, independent of environmental effects (Lookhart and Finney, 1984; Cooke, 1984) rapid and low cost resolution by electrophoresis method, known sources of polymorphism, a simple genetic control and various alleles are co-dominant, a complex molecular basis for genetic variability, and homologies between storage proteins that extend across taxa (see for review Cooke, 1984; Gept, 1990; Wrigley, 1992; Payne, 1987; Lafiandra *et al.*, 1993). Seed storage protein markers have also been indicated to be tightly linked with many important agronomic characters such as seed size, glume color and pubescence, heading time, disease and pest resistance, frost hardiness and plant height (see Konarev *et al.*, 1979; Metakovsky *et al.*, 1990 for review).

The above mentioned merits of storage proteins as markers lead to a more detailed marking of genotypes than is possible with the use of enzyme or morphological markers. Consequently, seed storage protein markers are being extensively used to resolve the actual botanic, genetic and breeding problems. Seed storage proteins have been used as markers for the analysis of genetic diversity within and among populations (Levy *et al.*, 1988; Ciaffi *et al.*, 1993;

Gregova *et al.*, 1997), plant domestication in relation to genetic resource conservation and breeding (Lafiandra *et al.*, 1993), genome relationships, especially in ploidy series (Konarev *et al.*, 1979; Kreis *et al.*, 1985), evaluation of phylogenetic relationships (Fernandez-Calvin and Orellana, 1990; Lafiandra *et al.*, 1993; Ladizinsky and Hynowitz, 1979), as a tool in plant breeding (Cooke, 1984; Payne, 1987; Wrigley, 1992). In wheat breeding, seed storage protein markers have been effectively used for accurate cultivar identification (Shewry *et al.*, 1978; Jones *et al.*, 1979; Cooke, 1984; Wrigley, 1992), selection of quality types (Payne, 1987), pedigree verification (Wrigley and Shepherd, 1977; Wrigley *et al.*, 1982), production of pure foundation seed, prediction of heterotic combinations and in the studies of the pattern and the level of genetic diversity and genetic relationship among adapted cultivars (Cox *et al.*, 1985b; Fabrizius *et al.*, 1988; Metakovsky *et al.*, 2000; Labuschagne *et al.*, 2000). The variation and amount and type of seed storage proteins is the main responsible factor for determining the differences in bread- and pasta-making quality and nutritional properties of flour derived from different wheat varieties (Payne, 1987; Lafiandra *et al.*, 1993). Protein markers could also be useful in the protection of intellectual property of new cultivars and documentation and variety description required in Plant Breeders Rights' application (Cooke, 1984; Wrigley, 1992.).

The effectiveness of storage protein markers as a means of classifying adapted cultivars and populations has limited the extent of isozyme marker application in wheat and barley breeding programs (Cooke, 1984). Although some workers (Konarev *et al.*, 1979; Cooke, 1984; Wrigley, 1992) argue that since genes are connected into genetic systems, protein markers can reflect the variability within that genetic system, which might range from a set of genes to the genome as a whole, storage protein markers fail to cover genetic information from the whole genome due to the limited number of loci that carry genes encoding for proteins compared to DNA based markers (see Gept, 1990 for review).

DNA-based marker data: Recently, a variety of DNA based marker systems have been developed for measuring genetic similarities in agricultural crop species (Schut *et al.*, 1997). DNA markers reveal polymorphism at the DNA level (Kumar, 1999). They have been proven to be powerful tools in the assessment of genetic variation within and between plant populations and in the elucidation of genetic relationships among adapted cultivars and accessions (Lee, 1995; Karp *et al.*, 1996). Currently, two types of DNA marker systems are available (Karp *et al.*, 1996; Gupta *et al.*, 1999): i) those that rely on hybridization between probe and homologous DNA segment(s) within the genome (restriction fragment length polymorphism: RFLP) (Beckman and Soller, 1983) and those that use polymerase chain reaction (PCR) (Mullis *et al.*, 1986) to exponentially amplify genome segments between arbitrary or specific oligonucleotide priming sites. The latter system includes, among others, random amplified polymorphic DNA (RAPD) (Williams *et al.*, 1990), simple sequence repeats (SSR) (Devos *et al.*, 1995) and amplified fragment length polymorphism (AFLP) (Vos *et al.*, 1995). Compared to morphological and biochemical markers, the DNA marker approaches are highly informative because: i) they allow direct comparison of genetic diversity to be made at the DNA level; ii) they have the potential to identify a large number of polymorphic loci with an excellent coverage of an entire genome; iii) they are phenotypically neutral; iv) they allow scoring of plants at any development stage; and v) they are not modified by environment and management practices (Tanksley *et al.*, 1989; Melchinger *et al.*, 1994; Messmer *et al.*, 1993). Compared with pedigree, DNA marker based diversity estimates better reflect the actual DNA differences among lines since selection pressure and genetic drift are accounted for (Barrett and Kidewell, 1998).

The DNA marker technique has been used to investigate the degree of genetic diversity and genetic relationships within and between cultivars and elite materials of wheat (Kim and Ward, 1997; Barrett and Kidwell, 1998; Barrett *et al.*, 1998; Bohn *et al.*, 1999). Although DNA marker systems directly measure DNA sequence variation among genotypes, results may be confounded by biased or incomplete genome coverage, detection of co migrating

nonhomologous fragments, or high crossover frequency between markers used in the evaluation and linked genetic material (Barrett and Kidwell, 1998). Some DNA marker techniques also require the use of hazardous radioactive isotopes (Tanksley *et al*, 1989; Bohn *et al*., 1999). Despite the great power they offer, DNA marker techniques are generally labor intensive, time-consuming and relatively expensive, so that sample sizes are usually small and the power to test statistical hypothesis is limited (Melchinger *et al*., 1991). Therefore, obtaining accurate DNA marker based genetic diversity and relationship estimates may require intensive screening efforts.

2.2. Effect of waterlogging on the physicochemical state of the soil

Gas exchange through diffusion and convective flow in well-aerated soils is fairly rapid (Armstrong, 1982). Diffusion of gases in soil depends on the amount and distribution of the air-filled pore spaces and most well aerated soils has an air porosity of 10 to 30% of its volume (Ponnamperuma, 1984). The diffusion rate of gases through water is about 10,000 and through wet soils is about 20,000 times less than the rate through the air (Armstrong, 1979, 1982).

When the soils become waterlogged, changes occur in the gaseous composition, pH, redox potential, and mineral content of the soil (Krizek, 1982). In waterlogged soils, water entering the gas spaces displaces O_2 and other gases, and thereby slows down or even interrupts the gas exchange between the atmosphere and the soil rhizosphere (Drew and Lynch, 1980; Sharma and Swarup, 1988, 1989). The depletion of the remaining available O_2 in the bulk soil, which leads to production of CO_2 (Setter and Belford, 1990), depends on the rate of respiration by roots and soil microorganisms (Setter and Belford, 1990), the rate of O_2 diffusion to the roots (Drew, 1983) and the temperature of the medium (Trought and Drew, 1982; Belford *et al*., 1985). The CO_2 concentration may reach 50% in the flooded acid soils and it may persist for several weeks (Ponnamperuma, 1984). Excessive CO_2 and deficient O_2 in the rhizosphere suppresses root growth for most terrestrial plants (Morord and Silvestre, 1996). Stolzy and

Letey in 1964 (cited in Sharma and Swarup, 1989) indicated that optimum crop root growth requires O_2 diffusion rates ranging from 25 to 40 x 10^{-8} g m^{-2} min^{-1}. The threshold O_2 concentration at which root extension begins to decrease is commonly reported to be about half that in air (Turner *et al.*, 1981).

Generally, well-aerated soils have redox potentials ranging from +400 to +700 mV whereas waterlogged soils have potentials ranging from -450 mV to +700 mV (Armstrong, 1982). In a greenhouse pot experiment conducted by Musgrave (1994), soil redox potential was reduced from an average of 409 to 149 mV due to waterlogging treatments. Working on Australian duplex soils, Thomson *et al.* (1992) also observed a reduction in soil redox potential from +600 to -200 mV due to 35 days of waterlogging. Stieger and Feller (1994) working on large pots embedded in the field observed that waterlogging of brown soils for 38 days decreased redox potential below zero compared to +350 mV in control pots. Leyshon and Sheard (1974) recorded a redox potential of +289 mV after 7-days waterlogging of silt loam soil. Davies and Hillman (1988) studied the redox potential changes under three different states of waterlogging, they observed that the redox potential was lowest (+85 mv) in continuous waterlogging, intermediate (+156 to +246) in transient waterlogging and highest (+442 mv) in the freely drained treatments.

The effect of waterlogging on soil pH is unpredictable. Generally, the pH values of most waterlogged mineral soils range between 6.7 and 7.2, but waterlogging increases the pH of acidic soils and decreases the pH of basic soils (Ponnamperuma, 1984). Laanbroek (1990) also indicated that waterlogging of high-pH soils with low organic matter content might not decrease the pH value below 8.0.

Waterlogging damage may be attributed more to the changes in the concentration of solutes in the soil water than to the direct effect of O_2 deficiency (Drew and Lynch, 1980). Following the restriction of gas exchange and subsequent depletion of O_2, some soil microorganisms make

use of electron acceptors other than O_2 for their respiratory oxidation (Drew and Stolzy, 1996; Armstrong, 1982) which sets a series of chemical and microbiological changes in the soil system (Ponnamperuma, 1984; Armstrong, 1982). These changes may be measured indirectly by the redox potential of the soil (Armstrong, 1982; Krizek, 1982). The reviews by Armstrong (1982), Ponnamperuma (1984), Krizek (1982) and Laanbroek (1990) show a rapid decrease of O_2 availability at 330 mV, nitrate (NO_3-N) at 220 mV, the appearance of soluble and reduced manganese (Mn) at 200 mV, iron (Fe) at 120 mV, disappearance of sulfides at –150 mV and appearance of methane at –250 mV. The capacity of a soil to transform nutrients plays a key role in the occurrence of nutrient deficiency or excess (Drew and Stolzy, 1996). Leyshon and Sheard (1974) in a greenhouse pot experiment using silt loam soil planted to barley observed no increase in the concentration of water soluble or exchangeable Mn in the soil due to 7-day waterlogging. Sharma and Swarup (1988, 1989) in field experiments conducted on alkaline soils of Indo-Gangetic Plains in India found a three to five fold increase in ammonium acetate extractable Fe and Mn in soil after six days of waterlogging. Waterlogging greatly enhances availability of Na (Sharma and Swarup, 1988, 1989) and the damage on crops due to excess levels of sodium chloride on saline soils (Barrett-Lennard *et al.* 1990). Stieger and Feller (1994) working on brown soil in large pots embedded in the field reported that continuous waterlogging of wheat during grain filling increased NH_4-N, Mn, and Fe, decreased NO_3-N, but observed no changes in Zn, Ca, K, Mg and P concentration in the soil. Availability of N decreases under waterlogging due to loss through volatilization and denitrification (Belford *et al.* 1985; Ponnamperuma, 1984). Waterlogging increases availability of P due to release of sorbed P into the soil solution as reduction of ferric phosphate to the more soluble ferrous phosphate increases (Phillips, 1998). While leaching is not likely to occur from waterlogged soil, phosphorus may become more readily available to plants for a short period during and after waterlogging (Patrick and Mahapatra, 1968). Due to their high solubility, Fe and Mn may accumulate to levels toxic for crop roots in waterlogged soils (Krizek, 1982; Stieger and Feller, 1994). Trought and Drew (1980b) observed a decrease in concentration of NO_3-N, Ca, K, and no clear trend in P, Mn, and Fe concentrations in soils due to waterlogging. Few

studies also reported an increase in the availability of S, Ca, Mo, Ni, Zn, Pb and Co in response to waterlogging of some soils (Krizek 1982; Ponnamperuma, 1984).

2.3. Effect of waterlogging stress on plant growth and development

Waterlogged soils have a profound effect on crop establishment and growth (Wenkert *et al.*, 1981; Fausey *et al.*, 1985; Hou and Thseng, 1991). Excessive water during germination causes the deterioration of seeds leading to decreased field emergence (Thseng and Hou, 1993; Hou and Thseng, 1991; Ueno and Takahashi, 1997). Germination and emergence of wheat were strongly retarded under anaerobic conditions (Cannell *et al.*, 1980; Thomson *et al.*, 1983; Ueno and Takahashi, 1997). Failure of seed germination under waterlogged conditions may have resulted from rapid absorption of water, which disrupts the cell membranes resulting in leakage of electrolytes, sugar and amino acids (Van Toai *et al.*, 1985; Hou and Thseng, 1991, 1992;). Poor emergence of seedlings from waterlogged soils has been attributed to reduced O_2 diffusion rates in the seed environments and hence to a reduction in the supply of O_2 to the seed and developing seedlings (Trought and Drew, 1980a). Under waterlogged conditions, the activity of microorganisms may also cause seed mortality as they may compete with the seed for O_2 or attack seeds by generating phytotoxic substrates or through pathogenic activity on seeds (Duczek, 1986). Pre-emergent seedlings are particularly susceptible to waterlogging stress since the seed has already been committed to germination but does not have the advantages of emergent leaves for carbohydrate production and respiratory process.

Soils can become waterlogged at any of the developmental stages of wheat crops. Gill *et al.* (1993) reported that the effect of waterlogging on wheat was serious when it occurred at the crown root initiation, flowering and grain filling stages. Cannell *et al.* (1980) concluded that for winter wheat the most sensitive stage to waterlogging stress was between germination and emergence; during this period, 16 days waterlogging killed all seedlings and six days waterlogging depressed plant populations to 12% (on clay soil) and 38% (on sandy loam soil)

of the control. Pre-emergence waterlogging caused severe damage to seedling establishment of wheat (Belford, 1981). Pre-emergence waterlogging halfway through germination gave more severe damage on emergence and growth of barley than near sowing date or near emergence (Shiel *et al.*, 1987). Sayre *et al.* (1994) reported a significant interaction between genotypes and the stage of crop development at the onset of waterlogging.

Roots require O_2 for respiration and other metabolic activities. Cannell *et al.* (1984) found that prolonged waterlogging reduced soil O_2 concentration by up to 90%. Meyer *et al.* (1985) found that root growth in wheat was reduced when soil O_2 levels fell to <15%, and ceased at <10% of the maximum in a well-aerated soil. Insufficient O_2 results in an anaerobic respiration, fermenting carbohydrate into alcohol and the production of only small amounts of energy (Drew, 1983). The limited energy produced is usually not sufficient for normal metabolism; hence many root cells die and decay under prolonged flooding of soils (Drew, 1983; Trought and Drew, 1982). Stressed roots show reduced respiration and total root volume (Watson *et al.*, 1976; Trought and Drew, 1982; Huang *et al.*, 1994a), lowered depth of penetration (Watson *et al.*, 1976), reduced nodal root growth (Trought and Drew, 1982), and cause death of seminal root system (Trought and Drew, 1982). It also showed increased resistance to transportation of water and nutrients through roots and increased number of adventitious roots emerging at root nods (Wenkert *et al.*, 1981; Gale *et al.*, 1984; Sharma and Swarup, 1988,1989; Huang *et al.*, 1995, 1997). In wheat, seminal root growth is particularly reduced, while nodal roots are much less affected by waterlogging of soils (Trought and Drew, 1980a; Thomson *et al.* 1992; Huang *et al.*, 1997). As all these effects on roots are reflected on shoot growth, tolerance of roots to such injuries is often regarded as an indicator of a plant ability to withstand waterlogging damage.

Typical effects of soil waterlogging on cereal shoots include reduced stand establishment, retarded leaf emergence and expansion; leaf wilting, rolling, yellowing and chlorosis, early senescence, and decline in overall growth rates (Krizek, 1982; Reid, 1977; Drew and Sisworo,

1977; Trought and Drew, 1980a, b). These symptoms, particularly wilting and chlorosis, suggest a reduction in water and nutrient uptake by waterlogged roots (Krizek, 1982; Trought and Drew, 1980a, b; Huang *et al.*, 1995; Sharma and Swarup, 1988,1989). Depressed absorption of water by wheat due to waterlogging has been reported by several workers (Gales *et al.*, 1984; Belford, 1981; Sharma and Swarup, 1989).

Waterlogging during tillering and stem elongation of wheat leads to fewer tillers, more floral sterility and fewer grains per spike compared to freely drained wheat (Watson *et al.*, 1976; Sayre *et al.*, 1994; Musgrave, 1994). Waterlogging at late stem elongation and grain filling of wheat significantly depressed floret fertility and survival (Belford, 1981). On alkaline and sodic soils, short-term (up to six days) waterlogging resulted in a reduced number of fertile tillers, length of ears and number of productive spikes (Sharma and Swarup, 1988, 1989). The adverse effects of waterlogging at early growth stages were reflected through reduced tillering and during grain filling through reduced grain weight and number (Watson *et al.*, 1976). Cai *et al.* (1994a) showed that 10 days waterlogging during grain filling reduced the number of green leaves on the main stem, chlorophyll content in upper leaves and grain dry mass. Waterlogging effect on number of grains per spike was greater for early than late maturing wheat genotypes (Gardner and Flood, 1993).

Waterlogging stress also has an adverse effect on phenological development of crops. Six days of waterlogging imposed after germination but before emergence delayed seedling emergence by about 11 days (Cannell *et al.*, 1980). Waterlogging stress also significantly delayed ear emergence and maturity, and reduced plant height (Watson *et al.*, 1976; Sharma and Swarup, 1988, 1989).

Waterlogging accelerates senescence of wheat plants (Drew and Sisworo, 1977; Trought and Drew, 1980b; Stieger and Feller, 1994; Cai *et al.*, 1994b). Both photosynthesis and translocation of carbohydrates are reduced in waterlogged plants (Kozlowski, 1984). In wheat,

Musgrave (1994) reported a significant reduction in flag leaf photosynthesis and stomatal conductance and demonstrated a strong association between apparent net photosynthetic rates and grain yields. An early rapid reduction in photosynthesis is largely the result of stomatal closure (Phung and Knipling, 1976). Limitations on photosynthesis through stomatal closure caused by waterlogging could restrict the amount of assimilate available for grain fill (Box, 1986). Huang *et al.* (1994a) reported that waterlogging reduced leaf water potential, stomatal conductance, photosynthesis and chlorophyll content of two wheat cultivars.

Waterlogging has been reported to reduce wheat yields by 0-74% (Grieve *et al.*, 1986; Gebre, 1988). Much of these variations have been explained by the length of waterlogging and stage of plant development at which waterlogging occurred. In India, short-term (six days) waterlogging in wheat resulted in grain yield reductions of 39 and 47% on alkaline and sodic soils, respectively (Sharma and Swarup, 1988, 1989). In Louisiana, USA, yield losses of 37 to 45% in the greenhouse and more than 50% in field environments have been reported by Musgrave (1994) and Musgrave and Ding (1998). In Great Britain, Cannell *et al.* (1980) reported yield losses of 18, 16 and 18% due to waterlogging before emergence, at early tillering and stem elongation stages of wheat development. In western Australia, Watson *et al.* (1976) showed that continuous and short intermittent waterlogging for 42 days in the first two months of growth reduced grain yields by 53 and 40%, respectively. Belford (1981) also reported a total yield loss of 19% due to waterlogging effects at seedling emergence, tillering and stem elongation stage. In field experiments on irrigated wheat, yield losses of 69 kg/ha was recorded in Australia (Melhuish *et al.*, 1991). In lysimeter studies, Cannell *et al.* (1984) showed that winter waterlogging at any time from the three tiller stage to late stem elongation reduced grain yield of winter wheat by 24 and 21% on clay and sandy loam soils, respectively. Studies at Griffith on a Riverina clay loam soil, in Australia, showed that three separate periods of waterlogging reduced yields by 44% (Meyer *et al.*, 1985). Adverse effects of waterlogging on wheat shoot dry matter and above ground biomass yields at maturity have been reported by several workers (Watson *et al.*, 1976; Trought and Drew, 1980 a, b; Belford,

1981; Cannell *et al.*, 1984; Gales *et al.*, 1984; Davies and Hillman, 1988; Sharma and Swarup, 1988, 1989; Van Ginkel *et al.*, 1992; Gill *et al.*, 1992; Sayre *et al*, 1994; Musgrave, 1994; Huang *et al.*, 1994 a, b). Yield losses up to 74% on experimental fields (Belayneh, 1986; Gebre, 1988) and 100% on low-lying farmers fields (Bechere *et al.*, 1994) have been observed on frequently waterlogged highland Vertisols in Ethiopia.

2.4. Effect of waterlogging on plant nutrient concentration and uptake

Mineral composition of cultivated plants under waterlogged conditions depends largely on soil oxygen availability. It has been indicated that soil waterlogging results in reduced foliage concentrations of N, P, and K in wheat shoots (Drew and Sisworo, 1979). Stieger and Feller (1994) reported that waterlogging during grain filling reduced grain yield as well as K, P, Zn and Mg concentrations and increased Mn and Fe in the straw and grains of wheat; the effect was greatest for the former nutrients in the grain and for the later in the shoots. Dechnik and co-workers in 1985 (cited in Stepniewski and Przywara, 1992) observed an increase in N and a decrease in P and Mg in winter rye grain and an increase in N, Ca and Mg in rye straw due to four weeks of waterlogging. In a greenhouse study using brown soil, Stepniewski and Przywara (1992) reported that uptake of N, P, K, Ca, Na and Mg by winter rye were reduced at a low O_2 concentration (cf. ODR values of 30 $\mu g\ m^{-2}s^{-1}$) induced by waterlogging. In a field study using wheat, Sharma and Swarup (1989) indicated that waterlogging of 25-days old wheat seedling grown on alkaline soils in the field reduced N, P, K, Ca, Mg, and Zn uptake and led to higher absorption of Na, Fe, and Mn by both straw and grain. Leyshon and Sheard (1974) obtained reductions in N, P, and K concentrations of 51, 61, and 58%, respectively, in barley seedlings exposed to short-term waterlogging conditions. Stepniewski and Labuda (1984) also in barley reported reduced N, P, and K nutrient concentrations in grains in response to 10 days' waterlogging stress. From a nutrient solution study, Huang *et al.* (1995) reported a reduced concentration of N, P, K, Mg and Zn in shoots and increased concentrations of these nutrients in the roots of winter wheat. On corn, Fausey *et al.* (1985) reported that six days flooding of corn reduced the concentrations of N, P, Ca, Mg and Cu in

the plant but increased the concentrations of Fe, Al, and Na. They also reported that K concentration peaked at two days of flooding then decreased, while Mn and Zn showed a reversed trend. Lal and Taylor in 1970 (cited by Fausey *et al.*, 1985) also reported that waterlogging decreased maize uptake of N, P, K, Zn, Cu, B, and Sr, increased uptake of Al, Fe, Mn, and Mo, and no change in the uptake of Ca and Mg. Several of the above reports have indicated that N, P, and K contents in seedling shoots, straw and grains were always more affected by waterlogging –induced O_2 deficiency than Mg and Ca contents. Trought and Drew (1980a) observed only a small net accumulation of N, P, K in the tillers more than in main wheat shoots. Calcium and Mg accumulated in both tillers and main shoots without being translocated from older leaves

Waterlogging accelerates nitrogen remobilization in the oldest leaves of young wheat plants (Trought and Drew, 1980; Stieger and Feller, 1994). Translocation of nutrients out of the senescing leaves to the younger emerging leaves is detectable within 2-4 days of anaerobic root conditions (Drew, 1983). In some other studies, however, the lower N status of waterlogged plants appears to be largely due to impaired root function rather the reduced nitrate availability (Drew and Sisworo, 1979; Trought and Drew, 1980). Many studies have documented that waterlogging or low O_2 damage may be fully or partially alleviated by the addition of fertilizer N (Trought and Drew, 1981; Watson *et al.*, 1976; Belford, 1981).

Waterlogging-induced O_2 deficiency may inhibit nutrient uptake and transportation in the sensitive crop varieties (Kozlowski, 1990) by altering root function due to root growth impairment (Trought and Drew, 1980; Drew and Lynch, 1980; Stepniewski and Przymora, 1992), by causing nutrient leakage due to reduced membrane integrity of root cells (Resen and Carlson, 1984) and inadequate energy for active ion uptake due to inefficient anaerobic metabolism (Setter and Belford, 1990; Barrett-Lennard *et al.*, 1990). However, ion uptake may continue through passive means (Drew and Sisworo, 1977).

2.5. Genetic variability for tolerance to waterlogging stress

Plants survive the damaging effects of waterlogging stress by either adapting to or tolerating the low O_2 concentration. Flood-tolerant plants adapt to anaerobic conditions by various mechanisms depending on species, varieties, growth stage and environmental conditions. This tolerance is associated with changes in morphological and anatomical structures, modifications in metabolic pathways and ability in compensatory growth habits (Belford, 1981; Kawase, 1981; Kozlowski, 1984; Blom *et al.*, 1990; Thomson *et al.*, 1990; Huang *et al.*, 1994a, b; Voesenek *et al.*, 1994). Krizek (1982) in his review has indicated that crop species and cultivars differed widely in their tolerance to waterlogging. Genetic variation and its association with evolution of plant adaptation to flooding were extensively reviewed by Davy *et al.* (1990). Soybeans are affected more by waterlogging than corn (DeBoer and Ritter, 1970). Corn and sunflower plants showed much less damage under prolonged flooding conditions than tomato and barley (Yu *et al.*, 1969). Hybrid corn cultivars were more susceptible to waterlogging stress than inbred cultivars at both pre-emergence and four to five leaf stage waterlogging stress (Fausey *et al.*, 1985). Winter wheat is more tolerant to waterlogging than winter rye or barley (Bourget *et al.*, 1966).

Genetic variation on seed flooding tolerance has been reported in corn (Wenkert *et al.*, 1981; Fausey *et al.*, 1985; Van Toai *et al.*, 1988), soybean (Hou and Thseng, 1991, 1992), sorghum (Thseng and Hou, 1993), and barley (Takada and Fukuyama, 1987) and highly tolerant varieties have been identified in barley (Takada and Fakuyama, 1987), soybean (Thseng *et al.*, 1996) and sorghum (Thseng and Hou, 1993). Large genetic variation in seed flooding tolerance among wheat varieties has been reported by Ueno and Takahashi (1997) and varieties from Japan and China (as they are well adapted to rice-paddy field) were found more tolerant to flooding than those from the Middle East, Greece or Sweden, as measured by percentage germination. In barley and soybean, tissues around a seed are considered related to the flooding tolerance (Takada and Fukayama, 1983; Hou and Thseng, 1991). In wheat,

however, seed flooding tolerance was reported to be associated with the amount of excreted ethanol, but not to seed coat color (Ueno and Takahashi, 1997).

Several studies have reported large differences among wheat genotypes in their ability to withstand prolonged, post emergence waterlogging stress (Thomson *et al.*, 1992; Gardner and Flood, 1993; McKersie and Hunt, 1987; Yu *et al.*, 1969). In North America, winter wheat cultivar Savannah was found more tolerant to waterlogging stress than cultivar Bayles (Huang *et al.*, 1994b) as measured by the amount of aerenchyma development in both seminal and the nodal roots. Using root to shoot sugar accumulation and biomass ratios as selection criteria, Huang and Johnson (1995) showed that the cultivar Jackson was more tolerant to waterlogging stress than Coker 9835. Based on yield performance under waterlogged and drained conditions in the greenhouse and rain shelter pot experiments, Musgrave and Ding (1998) found the cultivar Coker 9877 and advanced line LA 862 A16-8-3-X more tolerant to waterlogging stress than other cultivars and lines studied. In pot studies, the wheat cultivar Pato tolerated waterlogging stress better than the cultivar Inia; the tolerance associated with highest root porosities observed in Cultivar Pato (Yu *et al.*, 1969). Using the degree of crown root and aerenchyma formation and stomatal opening under hypoxia and resumption of seminal root growth and opening of stomata after termination of hypoxia, Huang *et al.* (1994a) found that cultivars Gore and Savannah were relatively the most tolerant to hypoxia, Coker 9766 and BR 34 were intermediate and Bayles and FL 302 were the most sensitive.

Three tolerant wheat genotypes (PRL/Sara, Ducula and Vee/Myna) were identified based on comprehensive screening, evaluation and yield trials of CIMMYT's bread wheat germplasm under field prolonged waterlogging conditions in Mexico. From these studies, yield levels ranging from 1.9 to 2.5 t/ha were obtained from these lines as compared to 1.57 t/ha obtained from tolerant check cultivar Pato (Van Ginkel *et al.*, 1992). These genotypes also performed well under waterlogging stress extended over different growth stages (Sayre *et al.*, 1994). In a one-year experiment conducted on a West Australian duplex soil, these genotypes, however,

did not perform any better than locally adapted cultivars (Condon, 1996). This could be attributed to the relative differences in the fertility of Australian duplex soil and the soils in Obrigon in Mexico, where these genotypes were initially screened. Under alkaline soil conditions in India, four of the 25 wheat varieties were found the most tolerant to both flooding and sodicity conditions (Gill *et al*, 1992). In another study, Gill *et al.* (1993) found that the cultivars CSW 538-2 and E 14-3 were relatively tolerant to waterlogging stress imposed at different growth stages under alkaline soil condition. Of 50 bread wheat cultivars evaluated for waterlogging stress, Lin *et al.* (1994) found varieties Zhemai 2, Nonglin 42, Zhengzhou 761 and Ningmai 6 most tolerant to the waterlogging stress imposed at stem elongation. Cao and Cai (1991) obtained grain yields of 4.5 to 5.25 t/ha and a 1000-grain weight of 43.8 g from a spring wheat tolerant advanced line Ning 8675 under prolonged waterlogging stress conditions. They also indicated that an advanced line FU 428 X 9-6-1-2, a spring variety Nonglin 46 from Japan and Pato from Argentina were highly tolerant to waterlogging stress.

Davies and Hillman (1988) studied vegetative growth and yield under continuous waterlogging of 4-week-old plants of various wheat species, and found that the hexaploid *T. macha* and tetraploid *T. dicoccum* were relatively the most tolerant to the waterlogging stress. Intervarietal differences in wheat seedling survival after seven days of flooding with cold treatments were reported by McKersie and Hunt (1987). In China, where waterlogging is a problem during the later stages of the crop cycle, Cao and Cai (1991) evaluated over 1000 landraces for tolerance and found that varieties Shuilaomai and Shuilizhan were most tolerant to the waterlogging stress. Some other studies have also reported that landraces were less sensitive to waterlogging stress than bred wheat cultivars (Cai *et al.* 1994a; Bechere *et al.*, 1994).

Genetic variation for tolerance to waterlogging stress has been reported to exist among wild relatives of wheat (see Forster *et al.*, 1993 for review). Taeb *et al.* (1993) evaluated a number

of *Triticeae* species for waterlogging tolerance and *Thinopyrum elongatum* and *Elytrigia repens* were shown to have better tolerance to the stress than wheat, as measured by shoot dry matter production, tillering and root penetration in waterlogged soils. In experiments with amphiploids, Forster *et al.* (1993) indicated that Chinese Spring (CS)/*T.elongatum*, CS/*T. scirpeum* and CS/*Secale montanum* produced the longest and most extensive root growth in waterlogged soils compared to that of the common wheat parent Chinese Spring. The amphiploid derived from CS and *T. elongatum* was remarkably tolerant to waterlogging stress, achieving much greater yields than the other wheat varieties studied (Akhtar *et al.*, 1994). Poysa (1984) evaluated tolerance of wheat to flooding using the 5A, 5B and 5D chromosome substitution lines of Cheyenne (CNN) into CS and found that following five days of flooding, only CS/CNN5D and Cheyenne had significantly better survival than CS, while all the substitutions and Cheyenne were more tolerant to seven days of flooding than CS. The above results demonstrated that genes in the wild species that code for waterlogging tolerance can express in a wheat genetic background and that wild species therefore have a potential to supply potent genes for improving waterlogging tolerance of wheat (Forster *et al.*, 1993). Villareal and Mujeeb-Kazi (1999) evaluated a wide array of CIMMYTs' synthetic hexaploid wheat germplasm (*T. turgidum* x *Aegilops tauchi* crosses) for tolerance to prolonged waterlogging stress under field conditions in Mexico. From this study, they found that five of 95 entries were tolerant to seven weeks of waterlogging stress as measured by percentage leaf chlorosis.

Several studies have located the chromosomes where the genes responsible for waterlogging tolerance traits are in wheat and its close relatives (Poysa, 1984; Forster *et al.*, 1993; Taeb *et al.*, 1993; Cao *et al.*, 1995; Boru, 1996). Using chromosome 5A, 5B, and 5D substitution lines of the cultivar CNN into CS, Poysa (1984) reported that genes controlling waterlogging tolerance to severe waterlogging stress are present in all the group 5 chromosomes. He further noted that with a moderate flooding stress, only the alleles in chromosome 5D in CNN differed from that of CS. Experiments with wheat-grass amphiploids and wheat-*T.elongatum*

chromosome addition lines showed that the genes for increased waterlogging tolerance were located on *T.elongatum* chromosomes 2E and 4E (Forster *et al.*, 1993; Taeb *et al.*, 1993). The effect of the 4E was a non-specific dosage effect which was also observed in tetrasomic 4B and 4D wheats, where as the effect of 2E was specific to the alien chromosome and was not observed in tetrasomic group 2 wheats (Akhtar *et al.*, 1994).

The presence of a few genes in grasses for anoxia tolerance was suggested by Mujer *et al.* (1993). Studies by Setter *et al.* (1996) (cited in Boru, 1996) have indicated that submergence tolerance in rice cultivars FR13A, BKNFR (76106-16-0-1-0) and Kurkaruppan was controlled by one dominant gene. In wheat, Cao *et al.* (1995), using the number of green leaves on the main stem, reported that waterlogging tolerance was controlled by a single dominant gene. Cao *et al.* (1992) earlier concluded that waterlogging tolerance in a highly tolerant cultivar, Nonglin 46, was controlled by one dominant gene. Boru (1996) working with CIMMYTs' tolerant lines (PRL/Sara, Ducula, and Vee/Myna) and susceptible genotypes (Seri-82 and Kite/Glen), reported a total of four major genes involved in waterlogging tolerance as measured by percentage leaf chlorosis, but tolerance in each genotype was governed by one dominant gene.

2.6. Combining ability and heterosis

Parental selection is the very first step in any plant-breeding program aimed at improving yield and related crop parameters. Sprague and Tatum (1942) introduced the diallel-crossing concept to the field of plant breeding by making all possible matings among a set of maize inbred lines. The diallel analysis has been the major mating design used by breeders to obtain information on value of varieties as parents, to assess the gene action involved in various characters, and thereby develop appropriate selection procedures and understand heterotic patterns of the progenies at an early stage of the hybridization program (Cukador-Olmedo *et al.*, 1997; Pickett, 1993; Virmani and Edwards, 1983; Saghroue and Hallauer 1997). With this regard, several workers (Wright, 1985; Sinolinding and Chowdhry, 1974; Dudley and

Moll, 1969) have made a reference to the value of the F_1 as a guide in the development of high yielding varieties from the cross. Griffing (1956) has developed a range of analytical techniques to generate information on the nature of genetic systems controlling the inheritance of economically important characters and heterotic responses of crosses.

2.6.1. Combining ability:

Combining abilities has been defined as the performance of a line in hybrid combinations (Kambal and Webster, 1965). Assessment of the combining ability could be useful to define the contribution of a variety to the performance of its progeny and mode of inheritance of a particular trait. Sprague and Tatum (1942) developed the original theory of combining ability and identified two components: general combining ability and (GCA) and specific combining ability (SCA). They defined GCA as the average performance of lines in a hybrid combination and that of SCA as deviations of certain crosses from expectations on the basis of the average performance of lines involved. General combining ability is largely due to additive gene effects and higher order additive gene interactions while SCA is largely a function of non-additive dominance gene effects and other types of epistasis (inter-allelic gene interactions) as well as genotype x environment interactions (intra–allelic gene interactions) (Cukador-Olmedo *et al.*, 1997; Griffing 1956; Widner and Lebsuck, 1973). Thus, significant values of GCA would be interpreted as indication of additive gene effects while that of SCA would be interpreted as indication of the predominance of non-additive gene effects caused by dominance and epistasis (Kambal and Webster, 1965).

Several workers (Gill *et al.*, 1972; Borghi and Perenzin, 1994; Boru, 1996; Cao *et al.*, 1994; Grant and McKenzie, 1970; Singh *et al.*, 1987; Shamsuddin, 1985; Larik *et al.*, 1995) have studied the effect of GCA and SCA in self-pollinated crops, particularly in wheat. The value of varieties as parents have been determined from estimates of GCA and SCA effects in a diallel crosses of winter wheat (Gyawali et al., 1968; Knobel *et al.*, 1997; Bitzer et al., 1982), spring wheat (Larik *et al.*, 1995; Pathak and Nema, 1983; Bhatt, 1971) and durum wheat

(Quick, 1978; Bechere and Tesemma, 1982; Ronga *et al.*, 1997). Studies on the relative magnitude of GCA and SCA have indicated that GCA is the principal source of improved grain yield in a hybrid combination (Borghi and Perenzin 1994, Brown *et al.*, 1966, Gyawali *et al.*, 1968, Morgan *et al.*, 1989, Bitzer *et al.*, 1982, Bechere and Tesemma 1982, Gill *et al.*, 1972). Virmani and Edwards (1983) and Pickett (1993) have concluded that GCA is much more important than SCA in the inheritance of yield and related traits in wheat. A number of recent large-scale trials have also shown that GCA is of greater importance than SCA (Pickett, 1993). However, Virmani and Edwards (1983) and Pickett (1993) in their review work have indicated that SCA becomes more important in spaced planting, as non-additive genes controlling SCA effects are not well expressed under competitive growing conditions

Sayed (1978) and Quick (1978) have studied GCA: SCA mean square ratio as an indicator of the nature of the genetic variability in a diallel analysis; high value of the ratio indicates the prevalence of additive genes while low value of the ratio indicates the prevalence of non-additive gene effects in determining a particular character. Baker (1978) suggested the relative importance of GCA and SCA could be assessed from the components of variance by expressing them as $2\delta^2_{GCA}/(2\delta^2_{GCA} + \delta^2_{SCA})$ ratio. The closer this ratio is to unity the greater the magnitude of additive genetic effects.

Many studies on combining abilities and inheritance of important characters of crop plants have been based on trials conducted under optimal growing conditions. In many parts of the world, however, wheat is produced under a range of abiotic and biotic stresses, particularly constraints related to edaphic conditions (Briggle and Curtis, 1987). Estimates of combining abilities across environments have indicated that both GCA and SCA effects for most characters interacted with the environmental change, but GCA was found to be more sensitive to environmental changes than SCA (Menon and Sharma, 1994; Singh *et al.*, 1987; Singh and Rana 1987; Chovatia and Jordan, 1989; Srivastava *et al.*, 1992). Mandal and Maity (1992) estimated combining abilities in wheat grown under different levels of boron toxicity. They

reported that values for GCA and SCA effects at different levels of B were variable in both direction and magnitude. Singh *et al.* (1987) working on wheat grown under rainfed and irrigated conditions reported that GCA effects were more sensitive to the changes in soil moisture conditions than SCA effects. In a six-parent diallel cross study, Singh and Rana (1987) found a strong salt stress influence on both GCA and SCA effects for salt tolerance characters in wheat. On the basis of combining ability effects, Singh (1988), Singh and Rana (1987) and Kathiria and Sharma (1986) were able to identify best combining parents to develop tolerant varieties for salt stress environments in India. These authors, however, noted that, unlike most estimates reported under optimal soil conditions, both GCA and SCA effects were important in the inheritance of most agronomic traits associated with salt tolerance characteristics in wheat.

Despite its worldwide importance, very few studies have been undertaken to identify and understand parental combining abilities and nature of inheritance of tolerance to waterlogging stress. Cao *et al.* (1994) and Boru (1996) have studied the inheritance of waterlogging tolerance in bread wheat using number of green leaves per main stem and percentage leaf chlorosis, respectively, as measures of tolerance. These authors reported that waterlogging tolerance was mainly controlled by additive gene factors. Thseng and Hou (1993) studied combining ability for pre-germination flooding tolerance in sorghum seed in a six-parent diallel crosses. They indicated that additive gene effects were more important than the dominance in the inheritance of pre-germination flooding tolerance as measured by germination rates, although the effects were significant in both cases.

2.6.2. Heterosis:

Heterosis (or hybrid vigor) was first introduced by Shull in 1907 to denote the stimulation in size and vigor in a hybrid. Heterosis, a genetic expression of the beneficial effects of hybridization, is usually described in terms of the superiority of F1 hybrid performance over some measure of the parental performance (Pickett, 1993; Stuber, 1999) such as the degree of

improvement in hybrid value over the mean of both parents (mid-parent heterosis: MPH) or over the best parent (high-parent heterosis: HPH) (Jinks, 1983). From a commercial point of view, heterosis (i.e., standard heterosis: SH) may be described as the degree of hybrid performance over the best available line variety (Virmani and Edwards, 1983). In wheat, Freeman first reported heterosis in 1919 (see Virmani and Edwads, 1983 for review).

Heterosis is a genetic phenomenon resulting from heterozygosity. Until recently, the underlying genetic basis of heterozygosity has not been satisfactorily explained despite many attempts to do so. Possible explanations were *dominance* (i.e., linked dominant favorable factors); *true overdominance* (i.e., single loci at which two alleles have the property that the heterozygote is truly superior to either homozygote), which is difficult to distinguish from *pseudo-overdominance* (i.e., nearby loci at which alleles having dominant or partially dominant advantageous effects are in repulsion linkage phase), and certain types of *epistasis* (i.e., interaction of nonalleles) (Lamkey and Edwards, 1999; Stuber, 1999). Burton (1968) stated that heterosis results from combined action and interaction of allelic and nonallelic factors and is usually closely and positively correlated with heterozygosity. Jinks (1983) presented heterosis as a function of loci at which the parents carrying different alleles, and the magnitude and net direction of nonadditive effects within or between those loci in a hybrid combination. According to Morgan (1998) and Pickett (1993), heterosis is brought about by bringing together in the F_1 the dispersed genes of dominant alleles showing directional dominance and nonallelic interactions, but not by heterozygote superiority or complementary epistasis. Flintham *et al.* (1997), however, noted that heterozygosity is an essential component of heterosis and it can arise when over dominance at a single locus is the major cause of heterosis. In a recent conference conducted on genetics and exploitation of heterosis in crops, scientists have reached to the conclusion that the dominance and epistasis are the principal genetic factors in the explanation of heterosis (Coors *et al.*, 1999).

Many studies have demonstrated heterosis for various characters of interest in inter-varietal crosses in wheat. Briggle (1963), Virmani and Edwards (1983), Wilson and Driscoll (1983) and Pickett (1993) reviewed heterosis in wheat and cited grain yields of up to 90% greater than higher yielding parents. In some cases, over 100% HPH have been reported in wheat (Pickett, 1993). Quick (1978) working with durum wheat cultivars and advanced lines representing an international array noted that four of the 55 hybrids studied displayed significant grain yield heterosis and the highest yielding parent was exceeded by 24%. Boland *et al.* (1985) reported a 113.4 MPH and 102.24% HPH yield increases from the commercial hybrid Titan released in Australia. In space-planted wheat, Morgan *et al.* (1989) cited early publications which indicated HPH of 20 to 30%, Martin *et al.* (1995) reported on average 9.2% MPH, and Larik *et al.* (1995) reported 17 to 75% MPH and 9 to 66% HPH for grain yield per plant. Menon and Sharma (1994) reported 89% heterosis for grain yield in one specific cross, which showed the highest SCA effects on grain yield. Standard heterotic effects higher than 88% were reported in early literature (Walton, 1971; Boland *et al.*, 1985). However, in the recent publications reviewed by Pickett (1993) and Jordaan *et al.* (1999), SH effects range from 10 to 20% over the best pure line variety. Morgan *et al.* (1989) and Borghi and Perenzin (1994) also reported SH effects of 5.9 and 3.3%, respectively, over the best pure line cultivar in wheat. Apart from grain yield, heterotic expressions on components of grain and whole plant yield have been investigated. Larik *et al.* (1995) reported a significant positive MPH and HPH for tillers plant^{-1}, grain number and spikelets spike^{-1} and harvest index in spring wheat. Morgan *et al.* (1989) reported that heterosis for mean TKW was positively correlated with heterosis for grain yield. These findings and the results reported by Rehman (1978) and Quick (1978) indicated that tiller number and grain weight were the components contributed significantly to the heterosis for grain yield in bread and durum wheats.

The extent of heterotic response of the F_1 hybrid largely depends on the breeding value and genetic diversity of the parents included in crosses, and on the environmental conditions under

which hybrids grown (Knobel *et al.*, 1997; Jordaan *et al.*, 1999; Bhatt, 1971; Young and Virmani, 1990). Cultivars are known to differ in their ability to combine with others when they are crossed. Identification of those specific combinations of parents is therefore essential in the exploitation of heterosis in agricultural crops (Briggle, 1963; Bhatt, 1971; Virmani and Edwards, 1983; Wilson and Driscoll, 1983; Jordaan *et al.*, 1999). Combining ability analysis of parents has been a useful guideline in wheat breeding programs to determine the practical value of cultivars or lines as parents for crossing and appropriate procedures to use in a breeding program (Dudley and Moll, 1969; Wright, 1985; Griffing, 1956). The GCA and SCA effects are important indicators of the potential value of parents in hybrid combinations (Ronga *et al.*, 1997; Saghroue and Hallauer, 1997; Cukadar-Olmedo *et al.*, 1997). Bhatt (1971) suggested that selection of parents for use in hybrid contribution first on the basis of GCA then followed by evaluation of specific effects on the subsequent generations would be an appropriate procedure to exploit heterosis in wheat.

Evaluation of combining ability and heterosis in the field or greenhouse is expensive and time consuming. As a result, genetic distance analysis has been used extensively as a guideline for selection of parents and prediction of heterotic response in crop plants (Shamsuddin, 1985; Cox and Murphy, 1990; Barbosa-Neto *et al.*, 1996; Martin *et al.*, 1995; Smith *et al.*, 1990). Heterosis is positively associated with genetic divergence of parents (Yadav and Murty, 1976; Bhatt, 1971; Grant and McKenzie, 1970). Morgan (1998) recorded the largest MPH for F_1 hybrids derived from parents with the largest phenotypic differences. Kronstad (1997) reported greater yield heterosis from winter x spring wheat crosses than for crosses within each group. Bitzer *et al.* (1982) studied hybrid vigor in high- and low-yielding eight-parent diallel crosses and reported MPH of 30% for low x low crosses, 25% for low x high crosses and 19% for high x high crosses. Liu *et al.* (1999) found MPH of 18.8% for grain yield and 9.7% for biomass yield from crosses of distant wheat parents. Theoretically, the more distant the parents, the greater the number of genes they differ by, the greater the potential interaction of the genes in the form of dominance and epistasis, thus the greater potential for heterosis

(Falconer and Mackey, 1989). Crosses between genetically distant parents are expected to yield a greater amount of heterosis in hybrids and large genetic variances among progenies in subsequent selfing generations than crosses of closely related parents (Messmer *et al.*, 1993; Cowen and Frey, 1987b; Cox *et al.*, 1985a). The genetic divergence of parents can be estimated either by coefficients of parentage (Martin *et al.*, 1995; Barbosa-Neto *et al.*, 1996; Cox and Murphy, 1990), or by genetic markers such as morphological traits (Cox and Murphy, 1990; Shamsuddin, 1985; Souza and Sorrells, 1991b), isozyme (Gizlice *et al.*, 1993; Smith *et al.*, 1990); storage proteins (Cox *et al.*, 1985b; Fabrizios *et al.*, 1998) and DNA based markers (Martin *et al.*, 1995; Messmer *et al.* 1993; Liu *et al.*, 1999; Bohn *et al.*, 1999).

Heterosis expression depends not only on the parental combinations but also on the effects of climatic, edaphic and management factors. Generally, heterosis is environment dependent, but the nature of interaction depends on the crop species, cultivars involved and the trait under consideration. Many studies have shown that heterosis is greater under stress environments than under favorable conditions (Axtell *et al.*, 1999; Virmani, 1999; Yadav *et al.*, 2000; Young and Virmani, 1990; Grant and McKenzie, 1970). Axtell *et al.* (1999) reviewed heterosis in sorghum and pearl millet and cited that yield of hybrid increased by 58% over the best parent under dry land conditions. Heterosis has been one of the major reasons for the success of hybrid wheat breeding program in the low-yielding, water-stress environments of the Southern Africa (Jordaan, 1999). Jordaan (1999) obtained yield heterosis ranging from 11.5 to 23.2% in winter wheat grown at low seeding rates and narrow row spacing in low yielding, moisture stress areas in South Africa. Grant and McKenzie (1970) reported that the magnitude of heterosis in wheat in the dry land environment was higher than those in the irrigated experimental condition. Yadav *et al.* (2000) found over 30% yield heterosis from landrace-based top cross hybrids of pearl millet under terminal drought stress. Rice hybrids have shown improved seedling tolerance to low temperature, and salt and submergence tolerance (see Virmani, 1999, for review). Research results reported by Young and Virmani (1990) also showed better adaptation of rice hybrids to stress environments. Under high

temperature and low moisture conditions in India, Pathak and Nema (1983) reported a highly significant HPH for grain yield plant^{-1} and grain number spike^{-1} in wheat. Rehman (1999) reported significant heterosis for grain yield and yield components of wheat under normal planting conditions, but not under late planting conditions. At present, information on the level of heterosis under waterlogged soil conditions is not available.

2.7. Variance components, heritability and correlations

2.7.1. Variance components:

Quantitative genetics is concerned about the variation expressed by quantitative characters. The amount of variation is measured and expressed in terms of variance (Falconer and Mackay, 1996). The total variance of a given character is its phenotypic variance (V_P) or the variance of phenotypic values. Plant breeders are usually interested in the partitioning of phenotypic variance into components attributable to different causes because such partitioning allows breeders to estimate the relative importance of various determinants of the phenotype. Environmental variance (V_E) is that part of the phenotypic variance attributed to environmental conditions (Falconer and Mackay, 1996). Environmental variance is the source of error in the genetics study and includes all the variations of the non-genetic origin; it reduces the efficiency of the selection process by obscuring the relationship between genotypes and phenotypes (Lynch and Walsh, 1998). The total genetic variance (V_G), also known as variance of genotypic value, is the part of the phenotypic variance, which can be attributed to genotypic differences among the phenotypes (Dudley and Moll, 1969). Genetic components of variance are of particular interest in applied breeding because they determine the rates at which characters responded to selection (Lynch and Walsh, 1998). The total genetic variance is further partitioned into additive genetic variance (V_A), dominance genetic variance (V_D) and epistatic genetic variance (V_I) (Dudley and Moll, 1969). The total additive genetic variance is the sum of the additive genetic variance contributed by individual loci; it is determined by gene frequency and by the average effect of substituting one allele from another (additive effect). Additive genetic variance is the variance of breeding values that

primarily cause resemblance between relatives and therefore determines the observable genetic properties of the population and response to selection (Falconer and Mackay, 1996). The dominance variance is the within-locus variance remaining after subtracting the additive variance from the total within-locus variance. The epistatic genetic variance is that portion of the total genetic variance, which remains after subtracting the total within-locus variance and represents the failure of the summation of the within-locus genetic variances to account for the total variation among genotypes (Dudley and Moll, 1969). A primary goal of any plant-breeding program is to develop and identify high yielding transgressive segregants. Populations with greater genetic variance are expected to produce higher yielding transgressive segregants than populations having lower genetic variance (Kisha *et al.*, 1997). Estimates of genetic parameters are useful to decide the appropriate breeding strategy that assists breeders to utilize the genetic variance present in a population. Estimates of various components of variance can therefore be used to calculate heritability, genetic correlations and predicted gains from selection (Saghroue and Hallauer, 1997).

2.7.2. Heritability

Allard *et al.* (1960) used the term heritability to specify the genetic portion of the total variability due to genetic causes. Heritability is a measure of the correspondence between breeding values and phenotypic values (Hanson, 1963; Jones, 1986; Falconer and Mackey, 1996). The term heritability has, however, two distinctly different meanings, depending whether it refers to genotypic values or to breeding values. The ratio of observed variation due to genetic variance (V_G) to the total phenotypic variance is heritability in the broad sense (h^2_b). Heritability in the broad sense expresses the extent to which individuals' phenotypes are determined by the genotypes. The ratio of additive portion (V_A) of the total genotypic variance (V_G) to the total phenotypic variance (V_P) is heritability in the narrow sense (h^2_n). Heritability in the narrow sense expresses the extent to which phenotypes are determined by the genes transmitted from the parents. Heritability in the narrow sense determines the degree of

resemblance between relatives and is therefore of greatest importance in breeding programs (Falconer and Mackay, 1996).

Heritability estimates provide an indication of the expected response to selection in a segregating population; as such they are useful tools in designing an effective breeding program (Burton and DeVane, 1953). In theory, both h^2_b and h^2_n can vary from 0 to 1. A high estimate, however, does not explain how good the breeding materials are. It rather estimates how well evaluation of parents will predict what the progenies will be like with a particular combination of breeding materials and techniques of evaluation (Jones, 1986). Characters with high h^2_n values can be improved more rapidly with less intensive evaluation than those with low values and hence are useful in making selection progress estimates. The h^2_b overestimates the response to selection as it includes non-additive effects (Dudley and Moll, 1969).

Heritability estimates are dependent on the method used to estimate them, the populations from which the estimates are derived, the unit of measurement and the environmental conditions encountered during the test (Hanson, 1963; Sidwell *et al.*, 1976; Jones, 1986). Quite large numbers of studies have been conducted to estimate both h^2_b and h^2_n for various characters of wheat grown in a wide range of environmental conditions (Alexander *et al.*, 1984; Sidwell *et al.*, 1976; Yildirim *et al.*, 1995). Heritability estimates for waterlogging tolerance and major agronomic characters of wheat under waterlogging condition are scarce (Boru, 1996).

2.7.3. Correlations

Characters of crop plants are generally correlated. Such correlations can be negative or positive. Correlated characters are of interest in plant genetics and breeding studies because of genetic causes of correlation through pleiotropic action of genes and changes brought about by artificial and natural selection (Falconer and Mackay, 1996; Lynch and Walsh, 1998).

Correlation between characters of crop plants may arise from environmental and genetic factors. Correlations resulting from environmental causes are overall effects of all the environmental factors that vary. The genetic causes of correlation are mainly pleiotropic effects of genes and gametic phase disequilibrium (linkage) between genes affecting different characters. Pleiotropy is the property of a gene whereby it affects two or more characters, so that if the gene is segregating it causes simultaneous variation in the two characters it affects (Falconer and Mackay, 1996).

Generally, three types of correlations are discussed in quantitative genetics and these are phenotypic, genotypic and environmental correlations. The association between two characters that can be directly observed is the correlation of phenotypic values, or phenotypic correlation (r_P). Phenotypic correlation measures the extent to which the two observed characters are linearly related. It is determined from measurements of the two characters in a number of individuals of the population. Genetic correlation (r_A) is the association of breeding values (i.e., additive genetic variance) of the two characters. Genetic correlation measures the extent to which degree the same genes or closely linked genes cause co-variation (simultaneous variation) in two different characters. The correlation of environmental deviations together with non-additive genetic deviations (i.e., dominance and epistatic genetic deviations) is referred to as environmental correlation (r_E) (Singh, 1992; Falconer and Mackay, 1996).

Correlation studies on various characters of crop plants are useful in deciding criteria for selection of the desired characters in the crop improvement program. Thus, estimation of the relative contribution of the different types of correlations has become an important tool in the applied plant breeding program. Singh (1992) and Lynch and Walsh (1998) discussed several methods used in estimating and testing statistical significance of correlations. Correlation coefficients may range in value from –1 to +1. Phenotypic correlations can normally be estimated with a high degree of accuracy. Estimates of genetic correlations, however, usually

have high standard errors because of difficulties to avoid the directional effects of confounding factors (i.e., dominance and epistatic genetic effects) on additive genetic correlation estimates (Lynch and Walsh, 1998). Furthermore, genetic correlations are strongly influenced by gene frequencies and therefore may differ markedly in different populations (Falconer and Mackay, 1996).

Knowledge of the mechanisms underlying the correlations between different characters is fundamental to understanding the constraints imposed on the selection process (Lynch and Walsh, 1998). Genetic correlations determine the degree of association between characters and how they may enhance selection. Depending on the sign, genetic correlations between two characters can either facilitate or impede selection progress. High values of genetic correlations may indicate considerable genetic association between the characters tested. Genetic correlations are useful if indirect selection gives greater response to selection for a character than direct selection for the same character (Falconer and Mackay, 1996).

Selection progress in any breeding program focusing on a specific production constraint may depend on the association between the various characters of crop plants. Many studies have estimated the association of characters in wheat grown under optimal environmental conditions (Sidwell *et al.*, 1976; Alexander *et al.*, 1984; Yildirim *et al.*, 1995). Grain yield in wheat is the product of number of spikes per unit area, average kernel weight and the number of kernels per spike. Many studies (Sidwell *et al.*, 1976; Alexander *et al.*, 1984; Yildirim *et al.*, 1995) have indicated that an increase in one component would result in an increase in total yield, provided there is no reduction in other components. Only few studies, however, have assessed both genotypic and phenotypic correlations in waterlogged wheat (Van Ginkel, 1992; Boru, 1996). Van Ginkel *et al.* (1992), working with waterlogged bread wheat germplasm under field conditions in Mexico, found that genotypic correlations for the association of grain yield with grains per spike and grain weight were significantly positive and those with percent leaf chlorosis (Chl), area under chlorosis progress curve (AUCPC) and productive spikes were

significantly negative. In a similar experiment, Boru (1996) also found significant negative genotypic and phenotypic correlations for the association of Chl and AUCPC-values with heading, plant height, biomass, kernel weight and seed yield in waterlogged F_3 bread wheat populations. Villareal Mujeeb-Kazi (1999), working with waterlogged synthetic hexaploid wheat germplasm in Mexico, reported negative phenotypic correlations coefficients for the association of Chl with yield per spike, kernel weight, grain filling period, plant height and spike length and positive coefficients with days to heading and physiological maturity.

CHAPTER III

GENETIC RELATIONSHIPS AMONG ETHIOPIAN BREAD WHEAT GENOTYPES BASED ON SEED STORAGE PROTEIN ELECTROPHORESIS

ABSTRACT

Wheat (*Triticum* spp.) is one of the principal cereal crops grown in Ethiopia. Research to determine seed storage protein composition and the level of genetic diversity among Ethiopian-grown bread wheat (*Triticum aestivum* L.) genotypes has not been conducted. Analysis of genetic relationships in crop species can provide a relative measure of genetic diversity, an index of parental selection and structure for stratified sampling of populations. The objectives of this study were to i) assess seed storage protein composition [i.e., gliadins and subunits of high molecular weight (HMW-GS) and low molecular weight (LMW-GS) of glutenin], ii) determine protein-based genetic distance estimates, and iii) search for clusters among 42 bread wheat genotypes from Ethiopia. The collection included the 38 most important genotypes released and advanced in Ethiopia since pre-1949 and four advanced CIMMYT lines.

Results from single kernel one-step sodium dodecyl sulfate-polyacrylamide gel electrophoresis (SDS-PAGE) indicated that there was a wide range of allelic variation in the composition of gliadins, LMW- and HMW-GS of the different genotypes studied. A total of 82 polymorphic bands (i.e., 32 gliadins, 35 LMW-GS and 15 HMW-GS bands) were detected among 42 genotypes. The HMW-GS, although it is a simple and straightforward technique, failed to distinguish adequately between all bread wheat genotypes. The gliadins and LMW-GS banding patterns were unique for all genotypes and hence were able to characterize adequately all genotypes studied. The mean protein based genetic distance estimate was 0.609 among genotypes with values ranging from 0.376 to 0.744. Over 80% of pair wise comparisons had genetic distance values between 0.55 and 0.700, indicating that genetic diversity among Ethiopian grown bread wheat genotypes was

fairly high. Cluster analysis based on genetic distance estimates also resulted in five distinct groups of genotypes. From this study it is concluded that the efficiency of Ethiopian bread wheat improvement program could be improved by cross-hybridizing parental genotypes, which are genetically far apart, and from different clusters.

Key words: Bread wheat; cluster analysis; genetic diversity, SDS-PAGE, seed storage proteins

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INTRODUCTION

Wheat has been and continues to be one of the most important cereal crops grown in the highlands of Ethiopia. Recently introduced bread wheat (*T. aestivum* L.) and indigenous durum wheat (*T. durum* Desf) are the two most important wheat species both in terms of area under cultivation and production (CSA, 1997). Bread wheat research in Ethiopia has shown the potential for selecting varieties with high yielding potential and responsiveness to improved agronomic inputs. Due to releases of high yielding (Gebre-Mariam, 1991), input responsive wheat cultivars (Tarekegne *et al.*, 1997, 1999), the yield potential has significantly increased (Tarekegne *et al.*, 1995) and the area under improved cultivars has substantially expanded (Payne *et al.*, 1996) mainly by replacing unimproved, low yielding input non-responsive landraces.

Genetic diversity in the available gene pool is the foundation for any crop improvement program because it helps to avoid crop vulnerability to pests and abiotic stress and to ensure continued selection gains (Messmer *et al.*, 1993; Barrett and Kidwell, 1998). In Ethiopia, however, variability in introduced hexaploid wheat is believed to be limited (Gebre-Mariam, 1991). As a result, bread wheat breeders often select parents for cultivar

development from highly adapted cultivars or from introduced elite materials. Crossing within such highly adapted germplasm, coupled with intense selection pressure, may lead to reduction in the level of genetic variation among parental lines, and consequently, reduction in selection gains. Moreover, farmers also restrict the level of diversity in adapted cultivars because they often refuse to change the old cultivars with new, improved ones owing to production constraints or quality considerations. Hence, breeders are concerned with the level and distribution of genetic diversity and relationship among adapted parents in bread wheats.

Information about genetic relationships among adapted cultivars has several important applications in crop improvement. Analysis of relatedness among cultivars provides a relative measure of genetic diversity in breeding stocks (Cox *et al.*, 1986; Souza and Sorrells, 1991a, b), an index for parental selection for establishing base populations (Manjarrez-Sandoval *et al.*, 1997; Bohn *et al.*, 1999), structure for stratified sampling of the population (Souza and Sorrells, 1991a, b), predictive measures of genetic variance and heterosis (Cowen and Frey, 1987; Manjarrez-Sandoval, 1997; Bohn *et al.*, 1999), major groupings of related cultivars, breeding materials and genetic resources (Messmer *et al.*, 1993; Graner *et al.*, 1994), and a means to monitor germplasm usage (Messmer *et al.*, 1993; Graner *et al.*, 1994).

Assessment of genetic similarity among cultivars has been based on the analysis of pedigree records (Cox *et al.*, 1986; Murphy *et al.*, 1986; Van Beuningen and Busch, 1997a), morphological traits (Cox and Murphy, 1990; Souza and Sorrells, 1991a; Van Beuningen and Busch, 1997b), biochemical markers (Cox *et al.*, 1985a; Souza and Sorrells, 1991b; Tsegaye *et al.*, 1994; Labuschagne *et al.*, 2000; Metakovsky *et al.*, 2000), and on DNA based markers (Siedler *et al.*, 1994; Barrett and Kidwell, 1998; Bohn *et al.*, 1999). In recent years, electrophoretically discernible seed storage proteins have been used to assess variation in cereal populations, landraces and modern cultivars (Cox *et al.*, 1985b; Souza and Sorrells, 1991b, Gregova *et al.*, 1997; Labuschagne *et al.*, 2000). Glutenins and gliadins are the two principal storage proteins in the wheat grain (Wall, 1979). Glutenins

have been shown to include subunits of high molecular weight (HMW-GS) and low molecular weight (LMW-GS) (Payne *et al.*, 1981; Jackson *et al.*, 1983). These proteins are primary products of structural genes (Wrigley, 1982) located at nine complex loci on the homoeologous chromosome groups 1 and 6 of wheat (Jackson *et al.*, 1983; Payne, 1987; Gupta and Shepherd, 1988; Metakovsky, 1991).

Storage proteins are highly polymorphic because of extensive allelism at their encoding genes (Payne *et al.*, 1981; Payne and Lawrence, 1983; Gupta and Shepherd, 1988; Metakovsky, 1991). Polyacrylamide gel electrophoresis in the presence of sodium dodecyl sulphate (SDS-PAGE) has been widely used to successfully identify allelic variants of all storage protein encoding genes (Galili and Feldman, 1983; Wrigley, 1992; Labuschagne *et al.*, 2000). The expression of allelic variants of storage proteins has been demonstrated to be independent of site, year and generation of seed production (Zillman and Buschuk, 1979; Wrigley, 1982, 1992). Moreover, gliadin variants have shown to be tightly linked to many important agronomic characteristics of wheat such as seed color, glume color and pubescence, heading time, disease resistance and frost hardiness (see Konarev *et al.*, 1979 for review). In addition, variants of glutenin have been shown to influence bread- and pasta- making quality (MacRitchie *et al.*, 1990). Because of these merits, allelic variants of storage proteins have been extensively used as efficient and reliable genetic markers in the genetic diversity and cultivar relatedness studies (Wrigley *et al.*, 1982; Cox *et al.*, 1985a; Souza and Sorrells, 1991b; Gregova *et al.*, 1997; Labuschagne *et al.*, 2000; Metakovsky *et al.*, 2000).

The objectives of this study were i) to characterize Ethiopian-grown bread wheat cultivars and lines by electrophoretic profiles of seed storage proteins, and ii) to assess genetic relationship among cultivars and lines based on the storage protein banding patterns, iii) to identify clusters of cultivars with similar protein patterns to provide a structure for parental selection based on dissimilarity of protein profiles.

MATERIALS AND METHODS

***Wheat cultivars*:**

A total of 42 bread wheat genotypes, 38 released and advanced lines from Ethiopia and four CIMMYT advanced lines kindly provided by Dr. Thomas Payne, were examined for gliadin and glutenin (HMW and LMW) subunit compositions. Table 3.1 presents year of release and cross/pedigree of the genotypes used in this study. The released genotypes currently cover most of the area allotted to bread wheat production in Ethiopia and the advanced lines are new lines derived from the breeding program with a great potential for future release. All wheat materials were kindly provided by the wheat improvement program at Holetta and Kulumsa R. C. in Ethiopia and were multiplied from single spikes of each genotype in greenhouse in 1999 at the University of the Free State , South Africa.

Extraction of storage proteins:

Three classes of storage proteins were extracted from six samples of randomly selected single kernels of wheat from each genotype. Kernels were placed in a folded paper and crushed individually to a powder with a mortar and pestle. The ground kernels were then placed in 1.5-ml eppendorf tubes.

Glutenin proteins extraction: The sequential extraction procedure of Singh *et al.* (1991) was used to obtain HMW- and LMW-GS. In this procedure, gliadins were first extracted by heating each ground single kernel sample in 300-µl 70% aqueous ethanol at 60 °C in a waterbath for 1 hr; it was then removed. The residue in each eppendorf tube was then washed twice by adding 1-ml 50% n-propanol, incubated at 60 °C for 30 min. briefly vortexed, then all n-propanol was sucked off after centrifugation at 10,000 rpm for 2 min.

Table 3.1. Ethiopian-grown bread wheat genotypes used in the diversity study based on seed storage protein electrophoresis

Genotype	Year of release/ registration	Cross/selecion
Et- 13 A2	1981	UQ105 Sel. x ENKOY
MITIKE (HAR 1709)	1993	BOW28/RBC
K 6290-Bulk	1977	(AF.MAYO x GEM) x Romany
K 6295-4A	1980	Romany x GB-Gamenya
Enkoy	1974	[HEBRAND sel./(WIS 245/ SUP51)]//[FR-FN/Y)^2.A)
Romany B.C.	1974	NA
Kanga	1993?	MENCO/ (WIS245 x SUP51)/(FR-FN/Y)^2.A
Mamba	1973	(AF.MY48/WIS245 x UP51)x(FR-FN/Y)^2.A
Dereselign	1974	CI8154/2*FR
Israel	Pre- 1949	NA
Bonde	Pre-1949	NA
Salmayo	1966	NA
Lakech	1970	PJ62/GB55 (118156)
Pavon 76	1982	VCM//CNO/7C/3/KAL/BB (PAVON)
Dashen	1984	KVZ/BUHO//KAL/BB (VEERY 5)
Batu	1984	GLL/CUC//KVZ/SX (SUNBIRD)
Gara	1984	AU//KAL/BB/3/WOP (BOBWHITE)
HAR 407	1987	KVZ/BUHO// KAL/BB (VEERY 15)
HAR 416	1987	AU//KAL/BB/3/WOP (BOBWHITE 28)
KUBSA (HAR 1685)	1994	ND/VG9144//KAL/BB/3/YACO /4/VEERY #5 (ATTILA)
WABE (HAR 710)	1994	MRL/BUC
GALAMA (HAR 604)	1995	4777*2//FLN/GB/3/PVN
ABOLA (HAR 1522)	1997	BOW/BUC
TUSIE (HAR 1407)	1997	COOK/VEE//DOVE/SERI
MAGAL (HAR 1595)	1997	F3.71/TRM//BUC/3/LIRA
TURA (HAR 1775)	1999	ARO YR Sel.60/1989
SHINA (HAR 1868)	1999	GOV9/AZ//MUS/3/R37/GHL21//KAL/BB/4/ANI
Watera (HAR 1920)	2000	MON / VEE//SARA
Hawie (HAR 2501)	2000	CHIL/PRL
Simba (HAR 2536)	2000	PRL/VEE6/MYNA/VUL (PRINIA)
HAR 2192	2001 (candidate)	CM75113-B-5M-1Y-O5M-3Y-2B-OY (MILAN)
HAR 2508	2001(candidate)	BJY/COC//PRL/BOW
HAR 2534	2001 (candidate)	ND/VG9144//KAL/BB/3/YACO/4/CHIL
HAR 1706	AL$^+$	BOW "S"
HAR 1863	AL	BOW/URE
HAR 1901	AL	BUC /FLK //MYNA/VUL
HAR 2561	AL	PRL/VEE6/MYNA/VUL (PRINIA)
HAR 2563	AL	CHUM18//JUP/BJY
PRL/Sara	AL	FKN/3/2*FCR//KAD/GB54/4/BB/CHA/6/T_AST/4/TP //CNO67/NO/3/CNO67/7C/5/JUP
Vee/Myna	AL	KVZ/BUHO//KAL/BB/5/ND/WW//LEE/FN/3/N/4/TI-R
Ducula	AL	HUC/TI-R/3/ATR*2/7C//NAC/4/SARA
Pato Blanco	AL	CWI 35494

$^+$AL = advanced line

The HMW- and LMW-GS were then extracted from the gliadin-free residue by incubating at 60 °C in 120-µl extraction buffer [50% n-propanol in 0.08 M Tris-HCl (pH8.0) containing freshly added 1.25% (w/v) dithiothreitol). After a brief initial vortexing, samples were again incubated for one more hour at 60 °C in 120-µl extraction buffer containing 0.17% 4-vinyl-pyridine, vortexed brifly; after a brief centrifugation, the supernatants of all samples were collected in a new eppendorf tube.

Gliadin extraction: gliadin proteins were extracted from ground single wheat kernels by incubating for 1 hr at 60 °C in 300-µl extraction buffer [18% urea consisting of 1% 2-mercapto-ethanol (2-hydroxyethylmercaptan; β-Mercaptoethanol)], vortexted briefly at every 30 min. interval and after a brief centrifugation the supernatants were collected in a new eppendorf. The extracted samples of both glutenin and gliadin proteins were mixed with an equal volume of sample loading buffer composed of 0.08 M Tris-HCl (pH8.0), 20% (v/v) glucerol, 1.6% (w/v) sodium dodecyl sulphate (SDS) and 0.016% (w/v) bromophenol blue.

Polyacrylamide gel electrophoresis:

Separation of proteins was performed with sodium dodecyle sulphate-polyacrylamide gel electrophoresis (SDS-PAGE) as described by Wrigley (1992). The analysis was carried out in a discontinuous vertical slab gel unit, Hoefer SE 600 System (Hoefer Scientific Instruments, San Francisco, CA). The separating gel (14-cm wide x 12-cm long x 1.5-mm thick) contained 10.1% (w/v) acrylamide, 0.11% (w/v) bis-acrylamide, 0.354 M Tris-HCl adjusted to pH8.8 and 0.1% (w/v) SDS. The stacking gel (14-cm wide x 4-cm long x 1.5-mm thick) contained 4.5% (w/v) acrylamide, 0.068 (w/v) bis-acrylamide, 0.124 M Tris-HCl adjusted to pH6.8 and 0.1% (w/v) SDS. Gels were polymerised by 0.19% (v/v) N, N, N^1, N^1-tetramethylethylenediamine (TEMED) and 0.023% ammonium persulphate (APS). Immediately after pouring the stacking gel solution onto separating gel sandwiched in a pair of gel glass plate (Hoefer Pharmacia Biotech, Inc.), a 1.5-mm thick comb was inserted to form 20 sample wells in each gel. After overnight polymerization of the gel, 40-µl

protein samples were loaded into the stacking gel sample wells with a disposable-tip micropipette. Electrophoresis was run for at least 3hr at a constant current of 66 mA per gel. During electrophoresis, the temperature of the system was controlled at 15°C by circulating water using Multitemp II Thermostatic Circular. The runs were terminated when the tracking dye front had reached the opposite end of the gel.

Gel Staining:

Gel staining was done following the procedure developed by Wrigley (1992). Immediately after electrophoresis, gels were removed from glass plates and immersed for at least 1 hr in a fixing solution composed of acetic acid, methanol and distilled water at a 1:4:5 ratio by volume. Then, gels were stained overnight with a solution composed of 0.58% (w/v) Coomassie Brilliant Blue G 250 in a 14% (w/v) trichloroacetic acid containing 5%(v/v) methanol and 200-ml distilled water. The background coloration of the gel was removed by destaining the gels frequently in distilled water at room temperature before examination.

Gel analysis and interpretation:

The HMW glutenin subunits at each of the Glu-1 loci were identified based on the nomenclature proposed by Payne and Lawrence (1983). Assignment of HMW-GS identification numbers was based on comparisons with assignments of the reference varieties Tugela (2*, 7+8, 5+10) and Verbeterde Kenia (1, 17+18, 2+12) (Randall *et al.*, 1993). The stained gels of gliadin and LMW-GS were scanned with a Bio-Rad scanner connected to the computer program. The scanned images were saved as TIFF files. The migration distance of proteins, relative to the banding patterns of a reference cultivar Chinese spring, was obtained from a densitometry scans of the TIFF file for every replication of each cultivar using the Molecular Analyst Finger Printing System (BioRad Labs, Hercules, CA). Only bands with 15 or more intensity were accepted. The gliadin formula was developed for all genotypes following the procedure developed by Zillman and Bushuk (1979). The LMW-GS bands were related to the nomenclature system developed by Gupta and Shepherd (1988), respectively.

Statistical analyses

The term 'protein band' is used here to describe a set of co-migrating protein polypeptides of each storage protein classes when subjected to SDS-PAGE. A total of 82 polymorphic bands (i.e., 32 gliadin, 15 HMW-GS, 35 LMW-GS bands) were obtained across all genotypes analyzed. Polymorphic bands were scored as present (1) or absent (0) and entered into a binary data matrix for statistical analysis. Bands that were monomorphic across the entire set of genotypes were excluded from the statistical analysis.

Pairwise comparisons of genotypes based on both unique and shared bands, were employed to calculate genetic distance. Distance matrices for all pairs of genotypes were constructed from the binary data using Euclidean genetic distance method (Kaufman and Rousseeuw, 1990). The Euclidean distances are the square roots of the sum of squares of the distances between the multidimensional space values of the variables for any two genotypes.

Cluster analysis was performed on the genetic distance matrices generated by Euclidean distance method to reveal the patterns of genetic relationship among genotypes. Several sequential, agglomerative, hierarchical, non-overlapping algorithms were used. However, the unweighted pair group method with arithmetic averages (UPGMA) method appeared to give the most satisfactory clustering results with most genotypes included in clusters of similar size. A dendrogram was formed on the basis of simple average method to provide an overview of genetic relationships among genotypes studied. This algorithm initially assumes each genotype as a separate cluster and sequentially joins clusters based on an increasing average distance between each of the members, so that each member has equal influence on the final result (Kaufman and Rousseeuw, 1990). All statistical analyses were performed using NCSS 2000 computer package (Hintze, 1998).

RESULTS AND DISCUSSION

The SDS-PAGE electrophorogrames of the three main storage proteins of Ethiopian-grown bread wheat genotypes are presented in Tables 3.2 to 3.6. The bread wheat genotypes examined were essentially uniform in their make-up of the three major wheat seed storage proteins. None of the cultivars or lines showed indications of having different biotypes. Several studies have reported some degree of heterogeneity in hexaploid wheat cultivars analyzed using HMW-GS (Branlard and Dardevet, 1985; Lawrence, 1986; Morgunov *et al.*, 1990; Wang *et al.*, 1993; Nakamura, 2000;) and gliadin composition (Jones *et al.*, 1982). In this study, however, seeds from single spike were used for each genotype, which may explain the high degree of homogeneity for all three storage proteins determined in this study. Genetic uniformity is an important criterion to release new varieties and its acceptance to the growers and baking industry. In small cereals such as wheat, a thorough selection process through five to six generations usually achieves genetic uniformity in genotypes developed through conventional breeding.

HMW-GS composition of Ethiopian-grown bread wheats:

The HMW-GS has distinctly slower electrophoretic mobility than LMW-GS, and so can be easily identified. Depending on the cultivars and lines, the HMW-GS has resolved into four to five bands, each with a different electrophoretic mobility. In literature, however, three to five HMW-GS bands are commonly reported in hexaploid wheat cultivars (Payne and Lawrence, 1983; Lawrence, 1986; Nakamura, 2000). The different HMW-GS was identified using the catalogue of Payne and Lawrence (1983) by comparing their mobility with that of South African bread wheat cultivars determined previously (Randall *et al.*, 1993), which were usually placed adjacent to the samples. All the HMW-GS were clearly resolved by this technique, except, in some cultivars and lines, for subunit 2* and 2. With 10% acrylamide gel, subunit 2 coded at the *Glu-D1* locus has the same mobility as subunit 2* coded at *Glu-A1* locus, so that when a cultivars possess subunit 2+12 at the *Glu-D1* locus, it is not possible to distinguish between subunit 2* and 'null' at the *Glu-A1* locus

(Payne *et al.*, 1981; Lawrence, 1986). Therefore, 5% acrylamide gel, as used by a number of workers (Payne *et al.*, 1981; Lawrence, 1986, Margiotta *et al.*, 1988), was used to resolve the subunit 2 and 2*. In this procedure, subunit 2* has greater mobility than subunit 2, as shown by several other studies (Payne *et al.*, 1981, 1987; Lookhart *et al.*, 1993; Lawrence, 1986).

Table 3.2. Frequency of high molecular weight glutenin subunits among Ethiopian-grown bread wheat genotypes

Locus	*Subunit*	*Genotype (no.)*	*Frequency (%)*
1A	1	7	16.7
	2*	33	78.6
	Null	2	4.8
1B	6+8	1	2.4
	7+8	8	19.1
	7+9	24	57.1
	13+16	1	2.4
	17*+18	5	11.9
	17+18	3	7.1
1D	2+12	12	28.6
	5+10	30	71.4
Total	11	42	100

Table 3.3. HMW-GS composition of Ethiopian bread wheat genotypes

Group	*HMW subunits*			*Frequency (%)*	*Genotype*
	1A	1B	1D		
1	1	6+8	2+12	2.4	Enkoy
2	1	7+8	2+12	4.8	K 6295-4A, Pato Blanco
3	1	7+8	5+10	2.4	Bonde
4	1	7+9	5+10	4.8	Dashen, HAR 407
5	1	7+9	2+12	2.4	PRL/Sara
6	2*	7+8	5+10	7.1	K 6290-Bulk, Kanga, Mamba
7	2*	7+9	5+10	40.5	Israel, Batu, Gara, HAR 416, HAR 1685, HAR 1407, HAR 1706, HAR 1775, HAR 1863, HAR 1868, HAR 1901, HAR 1920, HAR 2192, HAR 2508, HAR 2536, HAR 2561, HAR 2563
8	2*	7+8	2+12	2.4	Romany B.C.
9	2*	17*+18	5+10	9.5	HAR 710, HAR 604, HAR 1522, Pavon 76
10	0	7+8	2+12	2.4	Et-13
11	0	17*+18	2+12	2.4	HAR 1595
12	2*	17+18	5+10	4.8	HAR 2501, Ducula
13	2*	7+9	2+12	9.5	HAR 1709, Dereselign, Salmayo, HAR 2534
14	2*	17+18	2+12	2.4	Laketch
15	2*	13+16	2+12	2.4	Vee/Myna

The frequencies of HMW-GS among Ethiopian-grown bread wheat cultivars and lines are presented in Table 3.2. A total of 11 different subunits were revealed in this study: three subunits at the Glu-A1 locus, six at the *Glu-B1* locus and two at the *Glu-D1* locus. At the *Glu-A1* locus, subunit 2* was the most frequent, as represented by 31 (78.6%) of the 42 genotypes studied. The remaining seven (16.7%) and two (4.8%) genotypes were found to possess subunit 1 and 'null', respectively, at the same locus. The frequency of the subunit 'null', which cannot be translated into protein bands that can be distinguished on the gel, was thus low in Ethiopian-grown wheat genotypes as compared to the high frequency expressed by genotypes grown in Afghanistan (Lagudah *et al.*, 1987), the Netherlands (Kolster *et al.*, 1993), Grait Britain (Payne *et al.*, 1987), Italy (Pogna *et al.*, 1989), China and Japan (Nakamura, 2000; Wang et al., 1993), Australia (Lawrence, 1986), Portugal (Igrejas *et al.*, 1999) and Slovakia (Gregova *et al.*, 1997). The most frequent HMW-GS at the *Glu-B1* locus was 7+9, as shown in 24 (57.1%) cultivars and lines surveyed. The subunit pairs of 7+8, 17*+18, and 17+18 were present in eight (19.1%), five (11.9%) and three (7.1%) genotypes studied, respectively. The component 17* in the subunit pair of 17*+18 has slower mobility in this technique than 17 in the subunit pair of 17+18. Using 10% acrylamide gel, Margiotta *et al.* (1988) also reported the subunit pair of 17*+18 in hexaploid wheat genotypes collected from Nepal. The subunits 7, 20, 13+19 and 14+15, which occur moderately frequently in bread wheat genotypes grown throughout the world (Payne and Lawrence, 1983; Pogna *et al.*, 1989; Igrejas *et al.*, 1999; Lagudah *et al.*, 1987) were absent in Ethiopian-grown bread wheat genotypes. Two genotypes, Enkoy and Vee/Myna, showed subunit pairs of 6+8 and 13+16, respectively. The latter subunit pair was reported to occur frequently in the South African wheat cultivars (Randall *et al.*, 1993). At the *Glu-D1* locus, only subunit pairs 5+10 and 2+12 were distinguished with a frequency of 71.4 and 28.6% in the 42 genotypes studied, respectively. The subunits 3+12, 4+12, and 2+10 that are commonly reported to occur in wheat cultivars grown in several countries (Nakamura, 2000; Wang *et al.*, 1993; Graybosch, 1992; Pogna *et al.*, 1989) were absent in Ethiopian-grown bread wheat genotypes.

Variation in the HMW-GS has been related to bread making quality in hexaploid wheat cultivars (Lawrence, 1986; Payne *et al.*, 1987; Pogna *et al.*, 1989; Wang *et al.*, 1993). This study has revealed that the bread making quality influencing subunits such as 2* and 1 at the *Glu-A1*, 7+9 and 7+8 at the *Glu-B1*, and 5+10 at the *Glu-D1* occur most frequently in Ethiopian-grown wheat genotypes. Several studies (Kolster *et al.*, 1993; MacRitchie *et al.*, 1990; Lukow *et al.*, 1989) have generally positively related these subunits of HMW-GS to a good bread making quality.

It has been demonstrated that HMW-GS composition is a useful system for wheat cultivar identification (Lawrence, 1986; Nakamura, 2000). The HMW-GS composition of cultivars and lines studied are shown in Table 3.3. A total of 15 different patterns were evident among the 11 subunits of HMW glutenin indicated in Table 3.2. Each pattern revealed four to five HMW subunits of glutenin bands. Based on the HMW-GS patterns, Ethiopian-grown bread wheat genotypes were subdivided into fifteen groups. The frequency of occurrence of the fifteen patterns in the 42 genotypes ranged from 2.4% (one genotype) to 40.5% (17 genotypes). Eight HMW subunit patterns controlled by complex Glu-1 loci were represented only by one genotype. Three subunit compositions, 1,7+8, 2+12; 1, 7+9, 5+10; and 2*, 17+18, 5+10, each represented by two genotypes, and subunit composition 2*. 7+8, 5+10 represented another three genotypes. Each of 2*, 17*+18, 5+10 and 2*, 7+9, 2+12 subunit compositions represented four genotypes and that of 2*,7+9,5+10 subunit pattern represented 17 genotypes.

LMW-GS composition of Ethiopian-grown bread wheats:

Subunits of LMW glutenin have an electrophoretic mobility distinctly faster than HMW-GS, and hence were easily identifiable. Depending on the genotypes used, SDS-PAGE resolved LMW subunits of glutenin into eight to 15 distinct bands with a clear distinction between fast and slow moving subunits. Laketch and HAR 1706 expressed the least number of bands (i.e., 8) whereas Dereseligne had the maximum number of LMW-GS bands (i.e., 15). A total number of eight, nine, 10, 11, 12, 13 and 15 bands were expressed by two (4.8%), six (14.3%), 15 (37.7%), 12 (28.6%), four (9.5%), one (2.4%), and by one (2.4%)

of the 42 genotypes studied, respectively. The majority of genotypes possessed 10 and 11 LMW-GS bands. In hexaploid wheat, two to 16 different bands of LMW-GS may be expressed in a single cultivar (Gupta and Shepherd, 1988; Denery-Papini *et al.*, 1995). Maartens (1999) reported eight to 22 LMW-GS bands in 147 South African bread wheat cultivars.

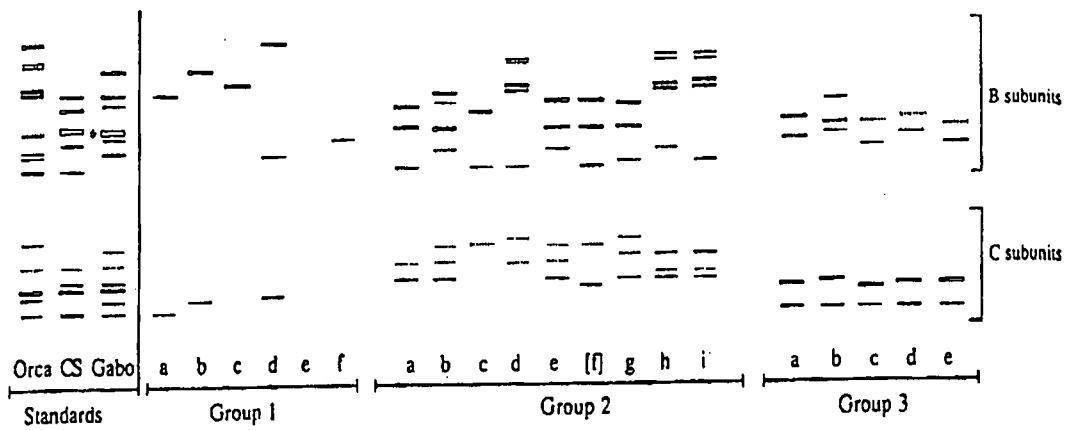

Fig. 3.1 Diagram showing the three groups of slow and fast moving subunit or subunit combinations along with standard cultivars (Orca, Chinese spring [CS] and Gabo) identified by two-step SDS-PAGE analysis of 222 bread wheat cultivars. Combinations 'a' and 'b' in each group are from Chinese Spring and Gabo, respectively. Direct evidence for the chromosomal location of pattern 'f' has not been obtained. Broken lines show faintly stained bands. * denotes that this thick band represents two bands of the same mobility, one controlled by 1BS and the other by 1DS in Chinese Spring and Gabo (Gupta and Shepherd, 1990).

The mobility of each band was determined using the Molecular Analyst Finger Printing System (BioRad Labs, Hercules, CA) by comparing with that of standard cultivar (Chinese Spring), which always runs adjacent to the samples. The banding pattern of each genotype was related to the nomenclature system developed by Gupta and Shepherd (1988).

Table 3.4. Frequency of LMW-GS banding combinations in the Ethiopian-grown bread wheat genotypes

Group	*Band combination*	*Genotype (no.)*	*Frequence (%)*
I	a	4	9.5
	b	6	14.3
	c	7	16.7
	d	1	2.4
	e	3	7.1
	f	11	26.2
	a/c	1	2.4
	a/f	4	9.5
	b/c	2	4.8
	b/f	2	4.8
	c/f	1	2.4
II	a	8	19.1
	b	1	2.4
	c	8	19.1
	d	0	0
	e	3	7.1
	f	4	9.5
	g	4	9.5
	h	0	0
	i	0	0
	a/c	1	2.4
	a/g	1	2.4
	c/g	3	7.1
	f/g	1	2.4
	e/g	1	2.4
	-------	7	16.7
III	a	8	19.1
	b	7	16.7
	c	8	19.1
	d	8	19.1
	e	5	11.9
	a/d	1	2.4
	b/d	2	4.8
	--------	3	7.1

-------- Represents LMW-GS band combinations, which did not match with the nomenclature system developed by Gupta and Shepherd (1988).

Table 3.5. LMW-GS composition of Ethiopian-grown bread wheat genotypes

Geneotype	*LMW-GS combination*			*Genotype*	*LMW-GS combination*		
	A1	B1	D1		A1	B1	D1
Et-13	a	c	c	HAR 604	f	c	----
HAR 1709	f	e	b	HAR 1522	b/c	e	b
K 6290-Bulk	f	e	b	HAR 1407	b	----	a
K 6295-4A	f	a	c	HAR 1595	b/f	a	b
Enkoy	c	----	c	HAR 1706	f	----	d
Kanga	b	c	a	HAR 1775	f	a	d
Romany	c	g	a	HAR 1863	f	----	a
Mamba	c/f	g	b	HAR 1868	a/f	a	b/d
Dereselign	b	g	a	HAR 1901	f	a	a/d
Israel	c	----	e	HAR 1920	c	e/g	e
Bonde	a	f	c	HAR 2192	b	a/c	c
Salmayo	c	f	c	HAR 2501	c	f/g	c
Laketch	f	----	a	HAR 2508	c	c	c
Pavon 76	b/c	c	a	HAR 2534	a/f	c	d
Dashen	b/f	f	d	HAR 2536	a	c	----
Batu	f	a	b	HAR 2561	f	c/g	b/d
Gara	b	a	e	HAR 2563	a/f	c	d
HAR 407	e	a	b	PRL/sara	a/f	c/g	d
HAR 416	a	----	d	Vee/Myna	f	c/g	e
HAR 1685	e	g	----	Ducula	a/c	a/g	a
HAR 710	e	b	e	Pato Blanco	b	f	d

-------- Represents LMW-GS band combinations, which did not match with the nomenclature system developed by Gupta and Shepherd (1988).

The catalogue presented in Fig. 3.1 had three groups of subunit combinations identified by two-step SDS-PAGE using 207 world collections of bread wheat cultivars. The three groups in the catalogue correspond to three *Glu-3* loci described by Jackson *et al.* (1983). The number of band combinations catalogued by Gupta and Shepherd (1988) are six, nine and five in group one, two and three, respectively. The relative frequency of the occurrence

of catalogued band combinations in the Ethiopian bread wheat genotypes are presented in Table 3.4. All the catalogued band combinations in group one (*Glu-A3* locus) were identified in 32 (76.2%) of the 42 genotypes studied; the remaining 10 genotypes showed two catalogued band combinations each. In group two (*Glu-B3* locus), six of the nine catalogued band combinations were present in Ethiopian wheats; combination 'd', 'h', and 'i' from the catalogue were absent in Ethiopian wheats. Seven genotypes, each showed two band combinations and the other seven genotypes had the banding pattern which did not match any of the catalogued nine combinations in the group two. In group three (*Glu-D3* locus), all band combinations in the catalogue were identified in 36 (83.3%) of the 42 genotypes studied. Three genotypes expressed two band combinations, and three others had banding patterns, which did not match any of the five catalogued band combinations in the group.

Table 3.5 presents the LMW-GS composition for 42 Ethiopian-grown bread wheat genotypes. The results indicated that all bread wheat cultivars and lines studied had unique banding patterns and band combinations of LMW-GS, indicating that LMW-GS pattern was efficient in discriminating genotypes compared to HMW-GS band patterns. Similar results were reported for South African bread wheat cultivars (Maartens and Labuschagne, 1999).

Gliadin composition of Ethiopian-grown bread wheats:

The SDS-PAGE separation of gliadin proteins extracted by 18% urea solvent produced straight and clear banding patterns for all genotypes and the differences between genotypes were distinctly unique. Each genotype was characterized by a formula that consisted of the relative distance traveled into gels, the number and the intensity of the protein bands, following the method of Zillman and Bushuk (1979). The electropherogram formulas determined for the 42 wheat genotypes listed in Table 6.1 are given in Table 6.6. In these formulas, only protein bands with an intensity value of 15 or more were considered. The mobility values of each band in each cultivar or line was determined in comparison with

that of Chinese Spring (standard) cultivar by averaging the mobility values obtained from six replications in duplicate gels.

The catalogue indicated that the total number of the different gliadin bands found in all genotypes was 32; most genotypes, however, possessed 16 to 18 different bands. In general, the number of bands found in the 42 genotypes ranged from the minimum of 14 bands found in K6290-Bulk, HAR 1920, HAR 2536 and Vee/Myna to 21 bands found in Et-13, HAR 1709, Romany B.C., K6295-4A, Dereselign and Israel. None of the cultivars or lines contained gliadin bands that migrated less than 43 units and more than 193 in the relative mobility scale into the gels. Most genotypes had gliadin bands, which moved between 43 and 188 units on the relative mobility scale.

Most genotypes were readily identifiable by their gliadin formula (Table 6.6) although some cultivars or lines are very closely related genetically to each other. None of the cultivars or lines studied produced identical gliadin banding patterns to one or more of the cultivars or lines. Dashen and Batu, however, gave similar gliadin patterns to that of HAR 407 and HAR 416, respectively. Hence, each cultivar or line had a unique gliadin composition and therefore could be easily identified using their electrophoretic formulas. De Villiers and Bosman (1993) reported a unique gliadin composition in South African bread wheat cultivars. Jones *et al.* (1979) also obtained a unique composition of gliadin for 73 out of 88 bread and durum wheat cultivars grown in USA; they found the remaining 15 cultivars to have identical or similar banding patterns to one or more other genetically closely related cultivars.

In this study, the slow-moving bands were the darkest and the fast-moving bands were the lightest in intensity. The intensity of the band mainly depends on the protein content of the samples (Zillman and Bishuk, 1979). Therefore, faint bands may not be used for cultivar identification purposes. Similarly, De Villiers and Bosman (1993) studying South African wheat cultivars suggested that band intensities should not be used for cultivar identification unless equal amounts of proteins across genotypes are used. In this study, proteins were

extracted from single whole seeds for all genotypes and, hence, band intensities should only be used to indicate the presence and concentration of protein in a band at a specific position on the mobility scale in the gel.

Table 3.6. Electrophoretic formulas of gliadin of Ethiopian-grown bread wheat genotypes

Cultivar	Mobility of bands relative to Chinese spring standard bands (30 40 50 60 70 80 90 100 110 120 130 140 150 160 170 180 190 200)
1. Et-13	5+ 5 3 3 2 3 3 2 2 2 3 1 1 1 2 1 1 1 1 1
2. HAR 1709	5 4 5 1 1 2 1 1 2 2 2 2 1 1 2 1 1 1 1
3. K6290-bulk	5 5 2 3 3 2 2 2 2 1 1 2 2
4. K6295-4A	5 5 5 3 3 2 1 1 2 2 2 1 1 1 1 1 1 1 1
5. Enkoy	5 4 4 5 4 5 2 2 2 2 2 2 2 2 2 1 2 1 1 1
6. Kanga	5 4 5 2 2 1 1 2 2 2 2 2 2 2 1 1 1 2 1 2 1
7. Romany B.C	5 5 5 1 1 2 2 2 2 2 1 1 1 1 1 1 1
8. Mamba	5 5 5 2 3 2 2 1 2 2 1 1 1 1 1 1 1
9. Dereselign	4 4 4 4 1 2 3 3 3 2 1 1 1 1 1 2 1 1 1 1
10. Israel	4 4 5 4 3 3 2 2 2 1 1 1 1 1 2 2 1 1 1 2 1
11. Bonde	3 5 5 5 3 2 3 2 1 2 2 1 1 1 1 2 1 2
12. Salmayo	5 4 5 4 2 2 1 1 2 1 1 2 1 1 1 1
13. Laketch	5 5 5 3 1 2 3 2 2 2 2 1 1 2 1 2
14. Pavon 76	5 5 5 3 2 1 2 2 2 1 2 2 1 2 1 1 1
15. Dashen	4 5 5 5 1 1 2 4 2 2 2 2 1 1 2 1 2 1
16. Batu	5 5 5 1 1 1 2 3 2 2 2 2 1 2 1 1 1 2
17. Gara	5 5 5 1 1 1 1 2 2 2 1 1 1 1 1 1 1 1
18. HAR 407	4 5 5 2 1 1 2 4 2 2 2 2 1 1 2 2 1 1 2
19. HAR 416	5 5 5 5 1 1 1 3 2 2 3 2 2 1 2 1 1 1 1
20. HAR 1685	5 5 5 5 1 3 2 3 2 2 2 2 1 1 1 3 1 2 2
21. HAR 710	5 5 5 5 2 3 2 2 1 1 1 2 1 1 1 2 1 1 1
22. HAR 604	5 5 5 3 2 2 2 1 1 2 1 1 2 2 1 1 1
23. HAR 1522	5 5 5 4 3 2 2 1 2 2 1 2 1 1 1
24. HAR 1407	5 4 5 1 1 5 2 1 2 2 1 1 1 1 1 1
25. HAR 1595	5 5 5 3 2 3 2 1 1 2 1 1 1 1 1 1
26. HAR 1706	5 4 5 1 1 2 3 2 1 2 1 1 1 1 1 2 2 1 2
27. HAR 1775	4 4 5 2 1 1 2 2 1 2 3 2 2 1 1
28. HAR 1863	4 5 5 1 1 1 2 3 1 2 3 1 1 1 1
29. HAR 1868	5 5 5 5 3 3 2 1 3 3 2 2 2 1 1 1 1
30. HAR1901	4 4 4 3 3 2 1 2 2 3 2 2 3 2 1 1 1 1
31. HAR 1920	5 5 5 2 1 1 2 4 1 2 3 3 2 1
32. HAR 2192	5 5 5 1 3 1 3 5 3 3 3 4 4 1 1
33. HAR 2501	5 5 5 5 3 3 4 1 2 3 1 1 1 2 3 3 1 1 1 1 1
34. HAR 2508	5 5 5 5 5 3 2 4 5 3 3 5 1 1 1 1
35. HAR 2534	5 5 5 1 3 2 2 4 5 2 3 3 2 2 1 1 2 1
36. HAR 2536	5 4 4 1 3 2 2 4 2 2 4 1 1 1
37. HAR 2561	3 3 4 3 2 2 3 4 2 2 2 3 3 1 1 1 1 1 1
38. HAR 2563	4 4 5 1 3 1 3 3 4 2 2 4 4 2 1 1 1 1
39. PRL/SARA	5 5 5 1 2 4 2 2 2 2 2 2 1 2 1 1 2
40. Vee/Myna	5 5 5 1 2 3 2 2 4 4 1 3 1 1 1
41. Ducula	5 5 5 1 2 2 1 3 2 1 2 3 3 1 1 2 1 2 1
42. Pato Blanco	4 5 5 5 1 3 4 2 3 1 1 2 3 1 2 1 2

+Relative band intensity, 1 represents the lightest band and 5 represent the darkest band. Scales at the top and bottom of the table indicate the relative position of a band on gel.

Estimates of genetic distance

A one-step SDS-PAGE analysis of seed storage proteins of the 42 Ethiopian-grown bread wheat genotypes generated a total of 82 polymorphic protein bands, i.e., 32 gliadin, 15 HMW- and 35 LMW-GS protein bands. The data matrix of these protein bands formed the basis for the Euclidean genetic distance calculations for all 861 pair wise comparisons of genotypes. Euclidean genetic distance may vary in values from 0 for two identical genotypes to 1 for two unrelated genotypes. In this study, a fairly extensive range of genetic distances was observed among the genotypes (Table 3.6). Genetic distance estimates ranged from 0.376 between HAR 2561 and HAR 2563 to 0.744 between HAR 1595 and HAR 2192, HAR 1595 and HAR 2508, and between HAR1595 and Simba. The mean genetic distance among all pairs of comparisons was 0.609. The standard deviation of the mean genetic distance was 0.058. The frequency distribution of genetic distance values for all 861 pairs of comparisons presented in Fig. 3.2 indicated that 80% of the pair wise comparisons had values between 0.551 and 0.700. Less than 1% and about 5% of pair wise comparisons had genetic distance values <0.450 and > 0.700, respectively. Estimates of genetic distance indicated the presence of a fairly high diversity among bread wheat genotypes in Ethiopia. The degree of relatedness or divergence between two cultivars or lines obtained based on protein bands was fairly corroborated to some extent by pedigree information presented in Table 3.1. Siedler *et al.* (1994) reported the average pairwise genetic distance estimates of 0.083 and 0.108 for European winter and spring wheats, respectively. Based on AFLP analysis of wheat cultivars grown in the USA, Barrett and Kidwell (1998) reported mean genetic diversity of 0.58 for spring x winter type pair wise comparisons, 0.53 within winter type and 0.49 within spring type. Bohn *et al.* (1999), using the combined data of the RFLPs, AFLPs and SSRS reported a genetic similarity of 0.53 to 0.87 with an average value of 0.63 in German and Austrian winter grown wheat cultivars. Cox *et al.* (1985) using gliadin protein bands reported genetic distance values ranging from 0 to 0.75 with a mean value of 0.44 in hard red winter wheat cultivars.

Table 3.7. Estimates of protein-based genetic distance for all pair wise combinations of 42 Ethiopian-grown bread wheat genotypes

Cultivar	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
1. Et 13	0.623	0.623	0.520	0.574	0.563	0.542	0.633	0.574	0.614	0.531	0.520	0.553	0.677	0.632	0.642	0.614	0.642	0.660	0.633	0.719	0.736	0.660	0.642	0.584	0.651	0.695	0.642	0.623	0.614	0.720	0.632	0.686	0.669	0.604	0.651	0.584	0.623	0.574	0.651	0.660	0.703
2. HAR 1709		0.574	0.594	0.584	0.594	0.632	0.623	0.520	0.604	0.642	0.574	0.623	0.614	0.520	0.553	0.623	0.574	0.614	0.564	0.623	0.711	0.669	0.594	0.574	0.642	0.632	0.669	0.594	0.660	0.623	0.695	0.677	0.660	0.632	0.677	0.651	0.669	0.604	0.542	0.669	0.623
3. K6290-Bulk			0.574	0.623	0.531	0.614	0.520	0.642	0.542	0.542	0.632	0.660	0.594	0.564	0.531	0.564	0.553	0.632	0.497	0.642	0.677	0.614	0.509	0.669	0.447	0.594	0.594	0.553	0.604	0.542	0.584	0.604	0.642	0.594	0.642	0.574	0.531	0.642	0.623	0.614	0.604
4. K6295-4A				0.520	0.632	0.533	0.623	0.604	0.564	0.642	0.594	0.564	0.574	0.604	0.651	0.564	0.574	0.686	0.623	0.711	0.677	0.651	0.633	0.614	0.623	0.633	0.614	0.594	0.623	0.623	0.660	0.677	0.677	0.574	0.677	0.594	0.632	0.564	0.642	0.633	0.584
5. Enkoy					0.642	0.660	0.669	0.614	0.651	0.634	0.542	0.594	0.604	0.632	0.711	0.686	0.623	0.695	0.669	0.669	0.719	0.660	0.694	0.584	0.614	0.711	0.728	0.660	0.686	0.736	0.686	0.614	0.703	0.677	0.703	0.677	0.711	0.614	0.614	0.660	0.669
6. Kanga						0.509	0.642	0.497	0.584	0.623	0.632	0.623	0.686	0.564	0.509	0.604	0.651	0.669	0.564	0.584	0.677	0.614	0.614	0.594	0.584	0.632	0.703	0.531	0.584	0.604	0.604	0.604	0.695	0.669	0.623	0.633	0.614	0.604	0.711	0.594	0.642
7. Romany B.C.							0.623	0.520	0.604	0.623	0.614	0.520	0.686	0.623	0.574	0.642	0.651	0.703	0.604	0.660	0.711	0.651	0.574	0.614	0.623	0.633	0.633	0.614	0.623	0.623	0.623	0.660	0.677	0.531	0.642	0.614	0.614	0.564	0.695	0.669	0.677
8. Mamba								0.651	0.553	0.509	0.584	0.594	0.584	0.531	0.497	0.509	0.642	0.520	0.531	0.632	0.651	0.677	0.584	0.660	0.509	0.542	0.584	0.584	0.632	0.633	0.553	0.633	0.485	0.623	0.574	0.642	0.604	0.574	0.686	0.677	0.614
9. Dereselign									0.594	0.651	0.542	0.553	0.677	0.574	0.564	0.614	0.695	0.660	0.594	0.651	0.736	0.695	0.642	0.520	0.594	0.623	0.695	0.584	0.633	0.614	0.651	0.686	0.720	0.623	0.614	0.677	0.695	0.574	0.686	0.695	0.703
10. Israel										0.614	0.584	0.632	0.584	0.594	0.520	0.509	0.584	0.642	0.531	0.594	0.614	0.584	0.473	0.642	0.553	0.584	0.542	0.584	0.614	0.614	0.614	0.614	0.594	0.642	0.574	0.584	0.604	0.614	0.614	0.642	0.669
11. Bonde											0.584	0.633	0.660	0.509	0.564	0.574	0.564	0.520	0.594	0.669	0.703	0.623	0.584	0.695	0.531	0.660	0.604	0.584	0.633	0.651	0.614	0.686	0.613	0.604	0.651	0.623	0.604	0.594	0.686	0.642	0.594
12. Salmayo												0.584	0.614	0.564	0.633	0.623	0.686	0.594	0.642	0.660	0.660	0.669	0.614	0.553	0.584	0.594	0.614	0.574	0.623	0.642	0.623	0.695	0.584	0.574	0.604	0.669	0.669	0.564	0.642	0.669	0.695
13. Laketch													0.642	0.594	0.542	0.574	0.660	0.642	0.651	0.633	0.720	0.604	0.623	0.497	0.574	0.623	0.623	0.604	0.634	0.669	0.633	0.651	0.633	0.623	0.651	0.642	0.642	0.553	0.651	0.604	0.651
14. Pavon 76														0.623	0.651	0.584	0.594	0.633	0.584	0.564	0.604	0.509	0.614	0.594	0.604	0.594	0.614	0.594	0.623	0.584	0.604	0.604	0.584	0.686	0.660	0.633	0.669	0.695	0.642	0.532	0.660
15. Dashen															0.447	0.574	0.584	0.542	0.509	0.614	0.651	0.642	0.564	0.520	0.574	0.584	0.660	0.520	0.594	0.614	0.669	0.669	0.633	0.660	0.651	0.677	0.642	0.553	0.669	0.604	0.485
16. Batu																0.542	0.594	0.574	0.520	0.623	0.642	0.594	0.531	0.594	0.497	0.553	0.633	0.509	0.604	0.604	0.623	0.642	0.604	0.669	0.542	0.614	0.594	0.542	0.642	0.614	0.604
17. Gara																	0.473	0.497	0.485	0.614	0.633	0.584	0.497	0.677	0.485	0.584	0.542	0.604	0.614	0.594	0.574	0.651	0.574	0.542	0.594	0.564	0.542	0.633	0.632	0.542	0.632
18. HAR 407																		0.531	0.520	0.642	0.642	0.594	0.553	0.703	0.542	0.614	0.574	0.614	0.604	0.623	0.642	0.642	0.642	0.614	0.660	0.532	0.532	0.623	0.604	0.574	0.584
19. HAR 416																			0.447	0.604	0.677	0.669	0.614	0.720	0.564	0.614	0.553	0.573	0.604	0.604	0.604	0.623	0.520	0.614	0.623	0.651	0.574	0.604	0.660	0.614	0.542
20. HAR 1685																				0.614	0.686	0.623	0.542	0.642	0.532	0.584	0.564	0.542	0.553	0.553	0.574	0.574	0.553	0.604	0.614	0.564	0.520	0.594	0.686	0.604	0.574
21. HAR 710																					0.553	0.520	0.642	0.604	0.614	0.564	0.623	0.564	0.614	0.614	0.651	0.594	0.614	0.695	0.633	0.711	0.695	0.686	0.686	0.604	0.651
22. HAR 604																						0.584	0.642	0.642	0.614	0.6034	0.642	0.604	0.574	0.686	0.651	0.594	0.633	0.660	0.614	0.623	0.642	0.686	0.669	0.677	0.669
23. HAR 1522																							0.574	0.574	0.584	0.632	0.651	0.553	0.660	0.642	0.642	0.677	0.660	0.703	0.677	0.594	0.633	0.711	0.623	0.560	0.711
24. HAR 1407																								0.669	0.520	0.594	0.553	0.632	0.642	0.584	0.584	0.660	0.604	0.594	0.623	0.531	0.553	0.623	0.623	0.614	0.677
25. HAR 1595																									0.677	0.651	0.736	0.614	0.660	0.726	0.744	0.711	0.744	0.720	0.744	0.703	0.703	0.604	0.660	0.651	0.660
26. HAR 1706																										0.542	0.623	0.564	0.553	0.594	0.509	0.614	0.594	0.584	0.553	0.564	0.542	0.553	0.632	0.604	0.669
27. HAR 1775																											0.485	0.460	0.473	0.473	0.497	0.623	0.473	0.613	0.473	0.532	0.574	0.623	0.694	0.651	0.660
28. HAR 1863																												0.531	0.497	0.473	0.497	0.564	0.391	0.485	0.497	0.531	0.553	0.623	0.677	0.633	0.623
29. HAR 1868																													0.447	0.497	0.520	0.564	0.564	0.651	0.584	0.553	0.594	0.623	0.660	0.574	0.604
30. HAR 1901																														0.553	0.509	0.553	0.553	0.542	0.574	0.520	0.542	0.632	0.719	0.660	0.633
31. HAR 1920																															0.485	0.574	0.509	0.542	0.531	0.564	0.604	0.651	0.703	0.623	0.632
32. HAR 2192																																0.509	0.406	0.564	0.460	0.497	0.564	0.614	0.669	0.642	0.703
33. HAR 2501																																	0.509	0.623	0.594	0.584	0.604	0.686	0.719	0.604	0.651
34. HAR 2508																																		0.564	0.434	0.542	0.542	0.594	0.686	0.642	0.651
35. HAR 2534																																			0.584	0.574	0.531	0.623	0.695	0.651	0.677
36. HAR 2536																																				0.542	0.584	0.574	0.686	0.677	0.669
37. HAR 2561																																					0.376	0.642	0.623	0.614	0.695
38. HAR 2563																																						0.642	0.623	0.594	0.604
39. PRL/SARA																																							0.651	0.711	0.594
40. VEE/MYNA																																								0.660	0.720
41. Ducula																																									0.623
42. Pato blanco																																									

Cluster analysis

The dendrogram from the UPGMA cluster analysis of the 42 bread wheat genotypes based on Euclidean genetic distances generated from seed storage protein bands is depicted in Fig. 3.3. The first bifurcation of the dendrogram separated the 42 genotypes into an upper cluster containing 29 genotypes and a lower cluster containing 12 genotypes; the upper cluster was dominated with modern, short stature genotypes whereas a lower cluster contained mostly old, tall genotypes. Estimates of Euclidean genetic distances ranged from 0.376 to 0.711 for an upper cluster and from 0.497 to 0.711 for a lower cluster. Pato Blanco was the most genetically distinct genotype and, hence, was clearly separated from all other genotypes studied. The next bifurcation in the upper group produced two clusters, each containing 24 and five genotypes with mean genetic distance estimates of 0.561 and 0.572, respectively. A further bifurcation of the lower cluster also produced two clusters, each containing 10 and two genotypes with means genetic distance of 0.572 and 0.542, respectively.

At 0.595 cut-off level, a cluster analysis resulted in a total of five distinct clusters, labelled as I, II, III, IV and V. Here, the choice to prune the dendrogram should be based on the compromise between the desire to have sufficiently homogeneous clusters (low within cluster genetic distance estimates) and the lowest number of small clusters. The phenon level chosen provided good resolution among clusters, as shown by fairly high co-phonetic value (0.895). High co-phonetic values indicate that the structure of the dendrogram was a good representation of the relationships among the different groups of genotypes. Co-phonetic values of 0.75 or more are usually recommended for the best fit of the cluster analysis (Kaufman and Rousseeuw, 1990).

In the Fig. 3.3, Cluster I contained five (11.9%) of the genotypes studied and spanned Euclidean genetic distance values ranging of 0.460 between HAR 1522 and Ducula to 0.677 between HAR 604 and Ducula with mean value of 0.561. This cluster further subdivided into two subgroups of three and two genotypes. Cluster II encompassed 12 (28.6%) of the genotypes with two further clear groupings of three and five genotypes;

estimates of genetic distance values range from 0.376 between HAR 2561 and HAR 2563 to 0.651 between HAR 1868 and HAR 2534 with mean value of 0.531. Cluster III also included 12 (28.6%) of the genotypes and contained genetic distance values ranging from 0.447 between HAR 416 and HAR 1685 to 0.642 between Mamba and HAR 407 and between Israel and HAR 416 with mean value of 0.539. There were three clear subgroups in cluster III, each encompassing four genotypes. Only two genotypes (Vee/Myna and HAR 1709) were grouped into cluster IV and contained a genetic distance value of 0.542. Cluster V consisted of 10 (23.8%) of the 42 genotypes and contained the genetic distance values ranging from 0.497 between Kanga and Dereselign and between Laketch and HAR 1595 to 0.660 between Enkoy and Romany B.C. and the mean genetic distance value was 0.572. Two clear sub-grouping were apparent in cluster V, each consisting of five genotypes. The standard deviation of 0.061, 0.056, 0.044 and 0.041 were calculated for all pairs of comparisons in cluster I, II, III, and V, respectively. Most old cultivars were grouped in cluster III and V, whereas, recently released modern genotypes and those in the pipeline were grouped in cluster II. Three of the leading genotypes (HAR 604, HAR 710, Pavon 76) were grouped in Cluster I. Several other studies have used seed storage protein electrophoresis to examine the level of genetic divergence among wheat cultivars (Wrigley *et al.*, 1982; Cox *et al.*, 1985a; Souza and Sorrells, 1991b; Gregova *et al.*, 1997; Metakovsky *et al.*, 2000; Labuschagne *et al.*, 2000). Cox *et al.* (1985) separated 43 hard red winter wheat cultivars into eight clusters based on genetic similarity estimates from gliadin PAGE patterns.

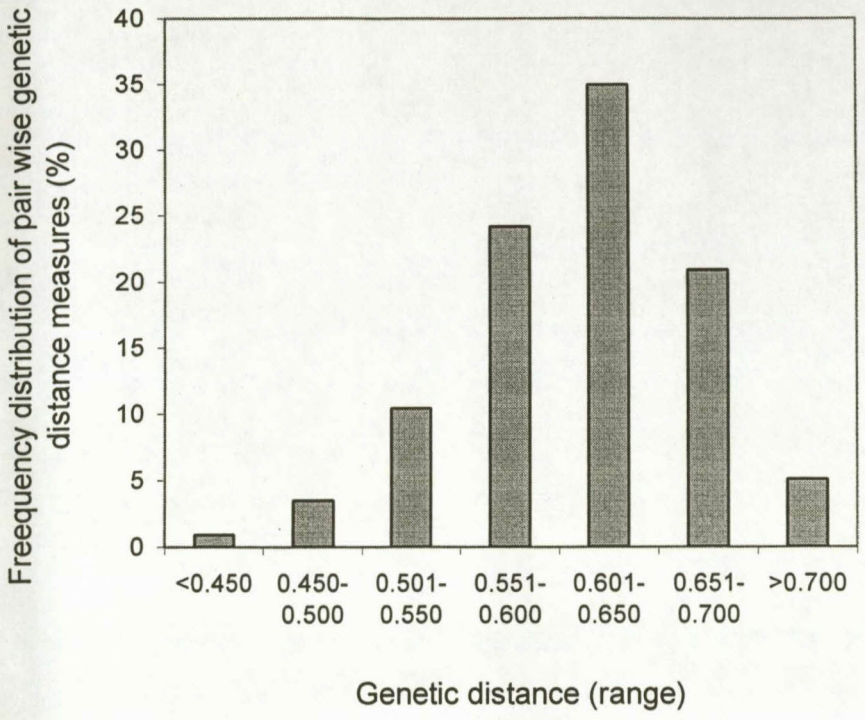

Fig. 3.2. Frequency distribution of 861 pair wise storage seed storage protein band genetic distance estimates among 42 Ethiopian-grown bread wheat genotypes.

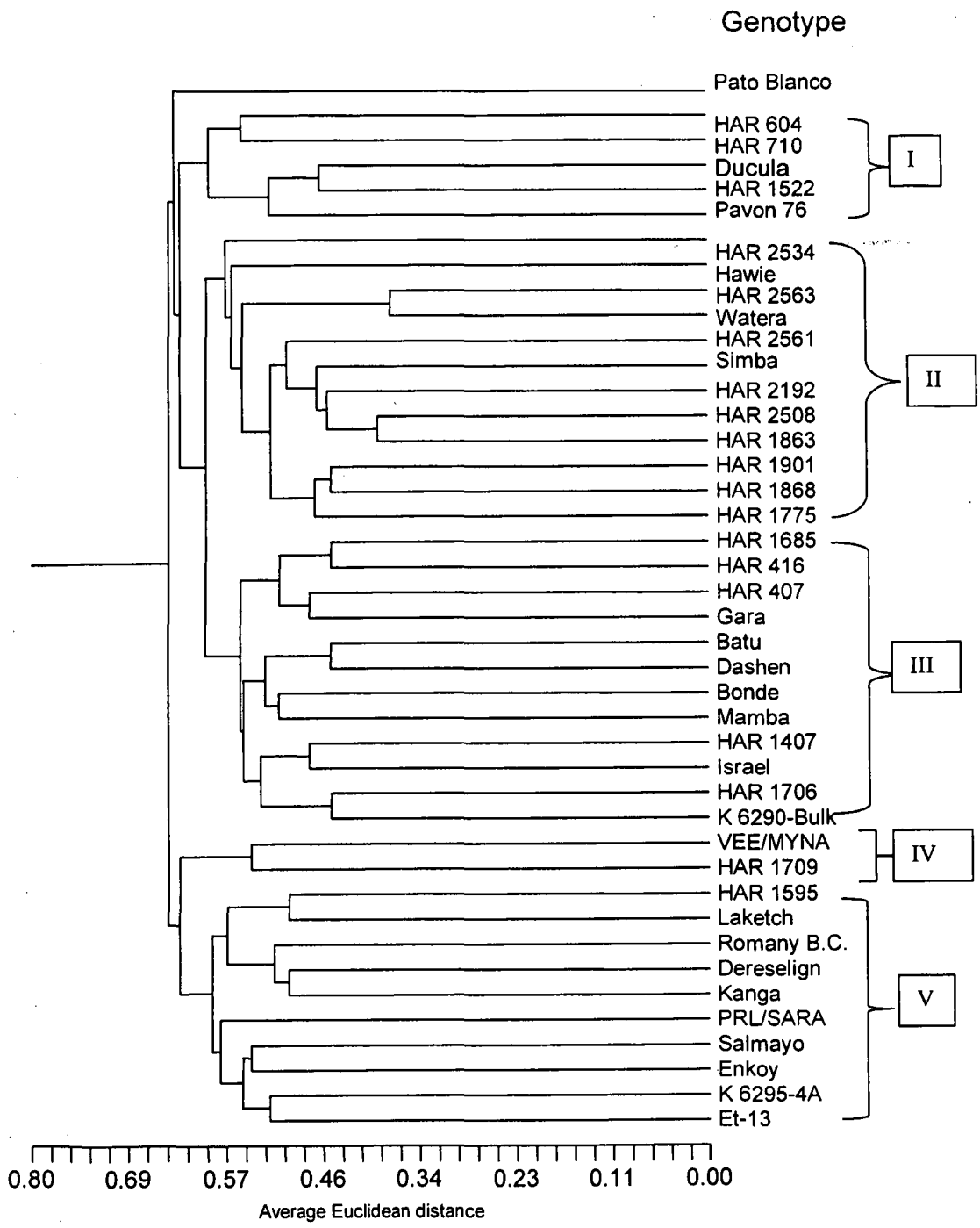

Fig. 3.3. Dendrogram depicting genetic diversity among Ethiopian bread wheat genotypes based on their electrophoretic patterns of seed storage proteins in the SDS-PAGE system.

CONCLUSIONS

Electrophoresis of seed storage proteins provides protein-banding patterns, which can be used to detect the level of variation among genotypes. In this study, a total of 42 bread wheat genotypes, 38 Ethiopian-grown and four advanced CIMMYT lines, were characterized based on their seed storage protein banding patterns in SDS-PAGE. The results indicated that single kernel one-step SDS-PAGE of proteins was efficient in detecting sufficient variability among genotypes studied, which can be used for cultivar identification, genetic resource management and for parental selection in a breeding program. Gliadins and LMW-GS were more efficient than HMW-GS in detecting the variation present among genotypes. As a result, gliadins and LMW-GS banding patterns were unique for each of the genotypes studied, whereas HMW-GS classified 42 genotypes only into 15 different groups. The high level of polymorphism detected in gliadin and LMW-GS could be the result of greater allelism at each locus encoding gliadin and LMW-GS proteins.

Knowledge of genetic diversity patterns and specific genetic distances estimates could increase the efficiency of wheat genetic improvement in Ethiopia by providing information on diversity among adapted parents for cultivar development and predictive measures on population genetic variances and heterotic responses. In this study, genetic distance estimates based on the protein bands indicated that the bread wheat gene pool in Ethiopia was fairly large with a mean genetic distance value of 0.609. The UPGMA cluster analysis based on genetic distances estimates separated the wheat genotypes into five distinct clusters. Therefore, cross-hybridizing genotypes from different clusters could provide populations with desirable means and large genetic variances, thereby improving the efficiency of breeding program in cultivar development.

The accuracy and ultimate utility of genetic distance estimates depends on the ability to identify the genetic variation among genotypes studied, which in turn, is directly related to the number of loci covered during an assay. Seed storage proteins, however, cover only a

limited number of loci in a genome. It is therefore suggested that combining protein data with DNA markers, pedigree information, and agronomic and morphological data could increase the power of genetic distance estimates in genetic diversity studies.

CHAPTER IV

EVALUATION OF BREAD WHEAT GENOTYPES FOR TOLERANCE TO WATERLOGGING STRESS

ABSTRACT

Soil waterlogging is a serious environmental stress affecting wheat (*Triticum aestivum* L.) grown in high rainfall or irrigated areas with heavy clay soils, Vertisols. Understanding genotype response to waterlogging stress is important for breeding tolerant genotypes. A greenhouse pot experiment was undertaken in 1998 to quantify the effects of different levels of prolonged waterlogging on grain yield and various other characteristics of wheat, to identify genotypes with better tolerance to the stress, and to identify plant characteristics associated with waterlogging damage which could be used as selection criteria in a breeding program. The experiment was laid out in a split plot design with four replications; three waterlogging treatments (free drainage: FD; transient waterlogging: TWl, and continuous waterlogging: CWl) were assigned to the main plots and 16 genotypes to the subplots.

The results indicated that increased severity in soil waterlogging stress significantly reduced grain yields, biomass yields, grains per spike and spikelets, kernel mass (KM), plant height and shoot elongation rate (SER), number of green leaves (GLN) on the main plants. It also delayed heading (DH) and physiological maturity (DPM), increased the percentage leaf chlorosis (Chl) at heading and the area under chlorosis progress curve (AUCPC) values. Continuous waterlogging resulted in greater damage to the plants in terms of most of the characteristics studied. The results of this study also demonstrated that there are marked genotypic differences among the bread wheat genotypes studied for tolerance to waterlogging stress and that genotypes differed in their reaction to waterlogging stress as indicated by significant genotype x waterlogging stress interactions on most of the characteristics studied. Ducula x1, PRL/Sara, HAR 604 and Vee/Myna were relatively tolerant to the waterlogging stress and ET-13 and K6290-Bulk were most sensitive. Under extreme stress conditions, grain yield was correlated positively with grains per spike and per spikelet, KM, biomass yield at

maturity (BYm), GLN, the stress tolerance index (STI), and negatively with Chl, AUCPC-value and stress susceptibility index (SSI). Percentage leaf chlorosis, BYm, grains per spike and per spikelet, and KM accounted for over 88% of the total variation in grain yield under continuous waterlogging. Heritabilities of these characteristics and indices were fairly large, indicating a promising gain from selection based on these characteristics. From this study, it is therefore, concluded that a good level of tolerance to waterlogging stress exists among the bread wheat genotypes studied and that breeding for tolerance can be facilitated by selecting genotypes with lower Chl, higher BYm, greater number of grains per spike and per spikelet, heavier KM, lower SSI and higher STI under continuous waterlogging conditions.

Key words: Genotype, tolerance, *Triticum aestivum*, waterlogging, and interactions

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INTRODUCTION

Soil waterlogging is a widespread environmental stress affecting crop production in high rainfall and irrigated areas throughout the world (Kozlowski, 1984; van Ginkel *et al.*, 1992). An estimated 10 to 15% of wheat in the developing world experience moderate to serious waterlogging stress due to temporary, transient or continuous ponding of excess water (Sayre *et al.*, 1994; Villareal and Mujeeb-Kazi, 1999). In the central and eastern African highlands, the incidence of soil waterlogging stress is most serious because of the widespread occurrence of poorly drained heavy clay soils, Vertisols (Debele, 1985; Jutzi and Abebe, 1986). Wheat in these regions is prone to serious injury and subsequent yield reduction because of high rainfall and low evaporative demand (Gebre, 1988; Simane *et al.*, 1999) during the months of establishment and vegetative growth (i.e., late June to early September).

Waterlogging may restrict plant growth by triggering oxygen deficiency in the soil (Trought and Drew, 1982; Cannell *et al.*, 1984; Ponnamperuma, 1984), altering nutrient

availability to plant roots (Trought and Drew, 1980b; Sharma and Swarup, 1988, 1989; Huang *et al.*, 1995a, b), or by allowing certain compounds to accumulate in the soil to phytotoxic levels (Ponnamperuma, 1984). The adverse effects of prolonged waterlogging stress on wheat includes poor germination and seedling establishment; restricted root growth and impaired uptake of nutrients; enhanced premature leaf senescence and drying; slowed rates of leaf emergence, elongation and accumulation of dry matter, reduced tillering, grain setting and grain weight; delayed maturation of plants, which finally result in a poor grain yield (Watson *et al.*, 1976; Cannell *et al.*, 1980; Trought and Drew, 1980a; Belford, 1981; Huang *et al.*, 1994a, b; Grieve *et al.*, 1986; Sharma and Swarup, 1988, 1989; Davies and Hillman, 1988; Thomson *et al.*, 1992; Gill *et al.*, 1993; Mian *et al.*, 1993; Cai *et al.*, 1994b; Musgrave and Ding, 1998). Depending on the duration of the stress and the crop development stage, waterlogging has been reported to reduce wheat grain yields by up to 73% (Luxmoor *et al.*, 1973). Estimates of yield losses due to waterlogging ranged from 15 to 20% in Britain (Cannell *et al.*, 1980; Belford, 1981), 40 to 50% in USA (Musgrave, 1994; Ding and Musgrave, 1995; Musgrave and Ding, 1998) and 40 to 55% in Western Australia (Watson *et al.*, 1975; Meyer *et al.*, 1985). In the highlands of Ethiopia, where waterlogging stress persists for about 50% of the crop growing season, yield losses in wheat ranges from 56 to 74% (Belayneh, 1986; Gebre, 1988).

Wheat productivity on soils susceptible to waterlogging may be increased by introducing efficient drainage systems (Belayneh, 1986; Jutzi and Abebe, 1986; Gebre, 1988; MacEwan *et al.*, 1992). Construction and implementation of drainage structures, however, may not always be possible as the required drainage system may sometimes be impractical and its economic viability is questionable because of the large investment required for the implementation of the system. Wheat production in frequently waterlogged areas, therefore, requires the development of cultivars that are more tolerant to prolonged waterlogging stress (Davies and Hillman, 1988; Van Ginkel *et al.*, 1992). Genetic differences for tolerance to waterlogging stress have been reported for wheat cultivars commonly grown in North America (McKersie and Hunt, 1987; Musgrave, 1994; Ding and Musgrave, 1995; Huang *et al.*, 1994a, b, 1995; Musgrave and Ding, 1998), China (Cai and Cao, 1990; He *et al.* 1993; Cai *et al.*, 1994 a and b;

Cao *et al.*, 1994, 1995), Australia (Thomson *et al.*, 1992; Gardner and Flood, 1993) and in India (Gill *et al.*, 1993). In Ethiopia, although wheat is one of the most important food grain grown on frequently waterlogged highland Vertisols, no research has been conducted to understand the response of adapted cultivars to prolonged waterlogging stress. Assessment of the response of genotypic variability to waterlogging stress is important in the selection of parental lines for developing tolerant genotypes and thereby improving wheat productivity in the frequently waterlogged highland Vertisol areas of the central and eastern regions of Africa, particularly in Ethiopia. This study was, therefore, undertaken to i) quantify the effects of different levels of waterlogging stress on grain yield and various characteristics of wheat, ii) identify bread wheat genotypes with better tolerance to waterlogging stress, and iii) identify plant characteristics associated with waterlogging tolerance which could be used as selection criteria in a breeding program.

MATERIALS AND METHODS

A greenhouse experiment was conducted in 1998 at the University of the Free State, South Africa to evaluate the tolerance of bread wheat genotypes to different levels of prolonged soil waterlogging stresses.

Experimental design and treatments:

This experiment consisted of three waterlogging treatments and 16 genotypes. The experiment was laid out in a split plot design with four replications. Waterlogging levels were the main plots and genotypes were randomised within waterlogging treatments and constituted the subplots. Split plot has been suggested as the best experimental design to conduct a waterlogging study in a greenhouse (Musgrave and Ding, 1998). The three waterlogging stress levels were i) a control without waterlogging stress therefore free drainage (FD), where seedlings grew in freely drained pots; ii) transient waterlogging (TWl), where seedlings grew in waterlogged pots for seven days followed by seven days of free drainage in three two-week cycles for a total of six weeks; iii) continuous waterlogging (CWl), where seedlings were subjected to permanently waterlogged

conditions for six weeks. Details regarding the source and pedigree of the genotypes studied are given in Table 4.1. Of the 16 genotypes, six were advanced lines from CIMMYT and were kindly provided by Dr. Thomas Payne, CIMMYT/EU East Africa Wheat Program. The other 10 genotypes were collected from Ethiopia and are currently grown widely in the country.

Table 4.1. Year of release or introduction, source and pedigree description of the bread wheat genotypes evaluated for tolerance to waterlogging stress in a greenhouse pot experiment, 1998

Genotype	Year of release / registration	Source	Cross/selection
DUCULA X1	AL	CIMMYT	HUC/TI-R/3/ATR*2/7C//NAC/4/SARA
DUCULA X2	AL	CIMMYT	HUC/TI-R/3/ATR*2/7C//NAC/4/SARA
DUCULA X3	AL	CIMMYT	HUC/TI-R/3/ATR*2/7C//NAC/4/SARA
DUCULA X4	AL	CIMMYT	HUC/TI-R/3/ATR*2/7C//NAC/4/SARA
PRL/SARA	AL	CIMMYT	FKN/3/2*FCR//KAD/GB54/4/BB/CHA/6/T-AST/4/TP// CNO67/NO/3/CNO67/7C/5/JUP
VEE/MYNA	AL	CIMMYT	KVZ/BUHO//KAL/BB/5/ND/WW//LEE/FN/3/N/4/TI-R
ET- 13 A2	1981	ETHIOPIA	UQ105 Sel. X ENKOY
K 6290-BULK	1977	ETHIOPIA	(AF.MAYO x GEM) x ROMANY
K 6295-4A	1980	ETHIOPIA	ROMANY x GB-GAMENYA
ISRAEL	Pre-1949	ETHIOPIA	NA
HAR 1709 (MITIKE)	1993	ETHIOPIA	BOW28/RBC
HAR 1685 (KUBSA)	1994	ETHIOPIA	ND/VG9144//KAL/BB/3/YACO/4/VEERY #5 (ATTILA)
HAR 710 (WABE)	1994	ETHIOPIA	MRL/BUC
HAR 604 (GALAMA)	1995	ETHIOPIA	4777*2//FLN/GB/3/PVN
HAR 1522 (ABOLA)	1997	ETHIOPIA	BOW/BUC
HAR 1407 (TUSIE)	1997	ETHIOPIA	COOK/VEE//DOVE/SE

AL = Advanced line; NA = not available.

Conduct of the pot experiment:

A soil sample from a virgin Vertisol with 3.12% organic matter and 46% clay content was collected from the top 20 cm depth layer from the Glen Agricultural College campus. The soil was pulverized and sieved to remove clogs and fibrous root materials, thoroughly mixed with nutrient solutions applied at a rate of 70 mg N as KNO_3 and 35

mg P as K_2HPO_4 kg^{-1} soil. This soil was used to fill three litre size polyethylene pots perforated at the bottom. Eight seeds of each genotype listed in Table 4.1 were planted in a pot on 28 February 1998, covered slightly with a thin layer of loose soil, and thinned to six seedlings after full emergence. All genotypes were allowed to establish themselves for 14 days under free draining conditions before the waterlogging treatments were imposed. When the seedlings reached three to four leaf stages, the pots destined for waterlogging treatments were each placed into a larger, six litre size non-perforated polyethylene pot (Fig. 4.1). Waterlogging was initiated by filling the outside pots with tap water and the water levels were maintained at 2-3 cm above the soil surface by watering every day throughout the treatment period. The freely drained control pots were watered to field capacity every day. During the duration of the experiment, N solution was applied to every pot at a rate of 0.5 mg N nutrient as NH_4NO_3 at two weeks intervals to avoid leaf chlorosis, which might be induced by N deficiency. Greenhouse temperatures were maintained at 15 °C minimum and 25 °C maximum.

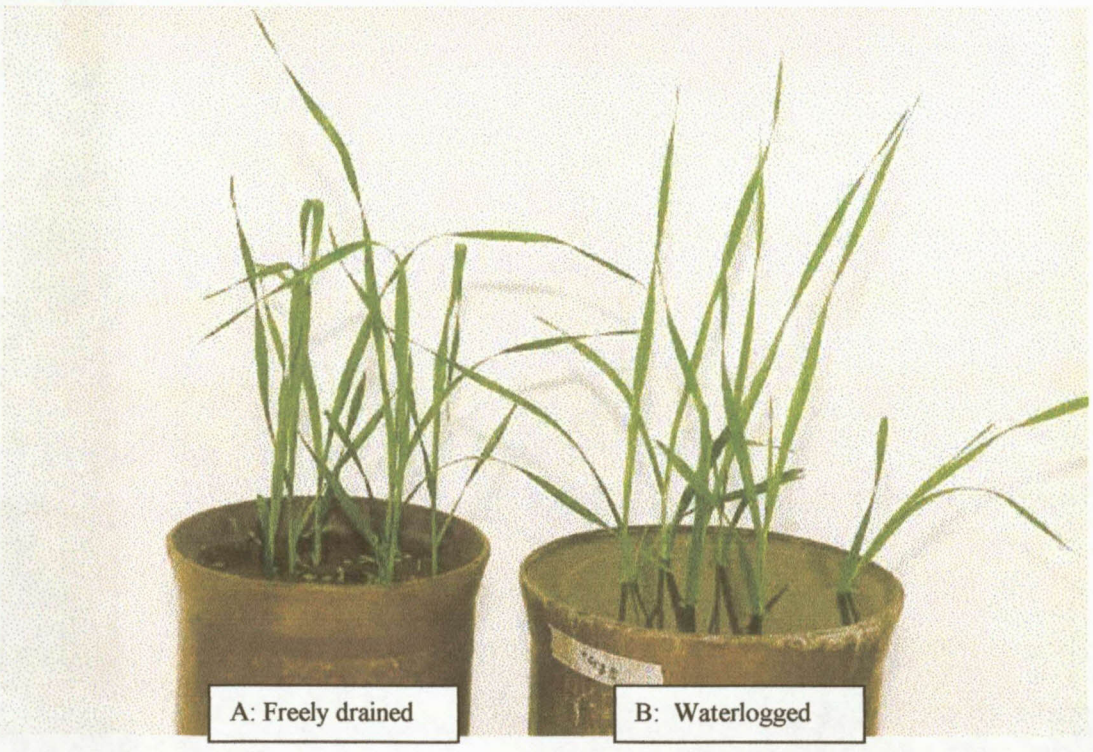

Figure 4.1. Pictures of 14-days old wheat seedlings (3-4-leaf stage) in a greenhouse pot experiment indicating the free drainage control (A) and waterlogging stress (B) (2 to 3 cm above the soil level) treatment applications.

Measurements:

The number of green leaves (GLN) on the four main plants per pot was counted every week, starting two weeks after waterlogging stress was imposed. During the waterlogging period, seedling height in centimetre from soil surface to the tip of the youngest leaf was measured on 11 occasions for all genotypes starting just before commencement of waterlogging. These measurements were also used to calculate seedling shoot elongation rate (SER: cm day^{-1}) for each genotype. For the waterlogged experiments, the percentage leaf chlorosis (Chl) was recorded weekly starting two weeks after the stress was initiated, from which the area under chlorosis progress curve (AUCPC) values were calculated using the formula: $AUCPC = \sum_{i}^{n-1}\left(\frac{x_i + x_{i+1}}{2}\right)(t_{i+1} - t_i)$ (Campbell and Madden, 1990), where n is number of assessment times with percentage leaf chlorosis score x at time t. At termination of the waterlogging treatment, plant height (PHv) was measured as distance in centimetre from the soil surface to the tip of the longest leaf. Two main plants (including tillers) were also cut at the soil surface, thoroughly washed with tap water, oven-dried at 60 °C for 48 hrs, then weighed to determine whole plant vegetative dry biomass yield (BYv). Days to heading (DH) and physiological maturity (DPM) were recorded as the number of days from planting to 50% ear emergence and complete yellowing of the mature plants, respectively. At maturity, the number of productive spikes per pot (PS) and spikelets per spike (SlPS) on the main plant were counted, and mature plant height (PHm) and average spike length (SLms) of main plant spikes were determined for all genotypes as a distance in centimetre from soil surface to the tip of awns and from the base of the first spikelet to the tip of the last spikelet, respectively. The remaining plants per pot were cut at the soil surface to determine the biomass yield (BYm), heads were separated into main spikes (ms) and tiller spikes (ts), hand threshed separately, then the resulting grains were weighed to determine grain yield per main plant spikes (GYms) and per tiller plant spikes (GYts), respectively. Total grain yield per pot (GYt) was determined as the sum of GYms and GYts and the total number of grains per pot (TNG) were determined by adding the number of grains obtained from the main spikes (GNms) and tiller plant spikes (GNts). Average kernel mass (KM: mg $grain^{-1}$) and number of grains per spike (GPSa) was determined by dividing GYt by TNG and TNG by PS, respectively.

Average number of grains per main spike (GPms) and tiller spike (GPts) was also calculated. The number of grains per spikelet (GPSl) was calculated as GPms ÷ SlPS. Yield based indices such as the stress susceptibility index (SSI) (Fischer and Maurer, 1978) and stress tolerance index (STI) (Fernandez, 1992) were calculated using the formula: $SSI = \left(Y_{FD} - Y_{WI}\right) \Big/ \left(Y_{FD} * \left(1 - \left(\bar{Y}_{WI} / \bar{Y}_{FD}\right)\right)\right)$ and $STI = \left[\left(Y_{FD}\right)\left(Y_{WI}\right)\right] \Big/ \left(\bar{Y}_{FD}\right)^2$, where Y_{FD} and Y_{WI} are yields of a genotype under free drainage and waterlogging (transient or continuous) treatments, respectively, $\bar{Y}_{FD}$ and $\bar{Y}_{WI}$ are mean yields of all genotypes under free drainage and waterlogging (transient or continuous) treatments, respectively. Broad sense heritability was calculated, considering genotypes and waterlogging treatments as random variables, as h^2_b = ([MSg-MSgxwl]/MSg)*100; where MSg and MSgxwl are ANOVA mean squares due to genotypes and interaction terms of genotype x waterlogging, respectively.

***Statistical analyses*:**

All measured characteristics were subject to the analysis of variance using *AGROBASE™* software (Argonomix software Inc., Canada) to assess the performance of genotypes under different levels of soil waterlogging stress conditions. Mean separation for those variables with significant *F*-values ($P \leq 0.05$) was accomplished following analysis of variance by using Fischer's least significance difference (LSD) test at $\alpha = 0.05$. Correlation between characteristics was tested using Pearson's Product Movement correlation with the NCSS 2000 computer package (Hintze, 1998). Stepwise regression analysis was performed using regression procedure of SAS (SAS Institute, Cary, NC) for three treatments separately to select the most contributing independent characteristics to the variation in the dependent variable, grain yield. The level of significance used to enter or delete a variable into a model by a stepwise selection procedure was $P \leq 0.10$.

RESULTS AND DISCUSSION

Grain yields:

The statistical significance and mean effects of treatments on grain yield parameters of bread wheat are presented in Table 4.2. Both waterlogging stress levels and genotypic differences exhibited significant effects on total grain yield (GYt: g pot^{-1}), grain yield per main plant spikes (GYms: g pot^{-1}) and tiller plant spikes (GYts: g pot^{-1}). Grain yields were significantly depressed with increasing severity in waterlogging stress. Relative to the freely drained (FD)-treatment, transient waterlogging (TWl)- and continuous waterlogging (CWl)- treatments reduced GYt by 24.4 and 35.7%, respectively. The corresponding figures for GYms and GYts were 26.6 and 21.4% under TWl- and 33.5 and 37.9% under CWl- treatment conditions. The reductions in grain yield obtained in this study were similar to those reported for waterlogged wheat under field studies in clay soils (Meyer *et al.*, 1985) and in sodic soils (Sharma and Swarup, 1988; Gill *et al.*, 1993) and under more controlled lysimeter studies using clay soils (Cannell *et al.*, 1980, 1984; Belford, 1981). The yield differences obtained in this study, however, were very low compared to the 40 and 55% yield reduction reported by Watson *et al.* (1976) on a duplex soil after 42 days of intermittent and continuous waterlogging stress, respectively, and 40 to 50% reduction reported by Musgrave (1994), Ding and Musgrave (1995) and Musgrave and Ding (1998) from prolonged waterlogging stress. In all three treatments, the correlation of GYt with GYts was strong compared to that with GYms although the coefficients between GYt and GYms increased with increasing severity in waterlogging stress (Tables 4.10 and 4.11). When averaged across the three treatments, HAR 604 was the highest yielding genotype followed by K6295-4A, HAR 1709 and six of the CIMMYT lines. K6290-Bulk and HAR 1522 had significantly the lowest mean GYt followed by ET-13, HAR 1407 and HAR 1685.

Mean GYms was significantly the highest for PRL/Sara, Ducula x1 and HAR 604, and mean GYts was the highest for K6295-4A, HAR 604, Vee/Myna, HAR 1709 and Ducula x3. Et-13, K6290-Bulk and HAR 1407 produced significantly the lowest mean GYms whereas HAR 1522 gave significantly the lowest mean GYts in this study. Broad sense heritabilities of 56.3% were calculated for GYt, which is somewhat lower than

values for most other simple characteristics. The corresponding values for GYms and GYts were 81.33 and 76.56%. Generally, heritabilities of complex characteristics such as grain yield are usually expected to be lower than those for simple characteristics because they are expected to suffer more from inflated error terms. The effect of waterlogging on the grain yield parameters differed among genotypes as indicated by significant waterlogging stress x genotype interactions (Tables 4.2 and 4.3). In addition, yields of the genotypes with the FD-treatment did not correlate significantly with yields from the TWl-treatment ($r = 0.209$) and CWl-treatment ($r = -0.037$), also reflecting differential response by genotypes to waterlogging stress. Furthermore, the yield ranges from the CWl- and TWl- treatments were greater than the ranges for the FD-treatment. Differential grain yield response obtained in this study are in line with findings of several other workers on wheat (McKersie *et al.*, 1987; Davies and Hillman, 1988; Cao and Cai, 1991; Thomson *et al.*, 1992; Van Ginkel *et al.*, 1992; Gill *et al.*, 1993; Gardner and Flood, 1993; Cai *et al.*, 1994a and b; Musgrave, 1994; Cao *et al.*, 1995; Ding and Musgrave, 1995; Musgrave and Ding, 1998). The effect of waterlogging severity on grain yield was less pronounced for HAR 604 and CIMMYT lines than for other genotypes (Table 4.3). These CIMMYT lines have been shown to yield over 2 t/ha under prolonged waterlogging stress in field conditions in Mexico (Van Ginkel *et al.*, 1992). Genotype HAR 604 is well adapted to regions prone to waterlogging stress in Ethiopia (Tarekegne, *et al.* 1999) and proved its highest ability in all three treatments in this study. Et-13 and K6290-Bulk were among the top four high yielding genotypes under FD- treatment condition, but they were the most affected and gave the least yields under waterlogging.

Table 4.2. Statistical significance and mean effects of treatments on grain yields, biomass yields, and components of yields of bread wheat, 1998

Treatment	GYt	GYms	GYts	BYm	BYv	PS	GPSa	GPms	GPts	SlPS	GPSl	GM	SLms
		g/pot		(g/pot)	(g/2plants)			(no.)				(mg/grain)	(cm)
Heritability (h^2_b)	56.25	81.33	76.51	77.01	72.85	85.34	92.25	72.43	80.90	88.24	63.05	77.31	95.89
Waterlogging (Wl)	***	***	***	***	***	*	***	***	***	Ns	***	***	*
FD	24.29 a	11.89 a	12.36 a	58.44 a	5.21 a	10.08 b	49.88 a	59.43 a	44.26 a	17.83	3.34 a	50.58 a	9.75 a
TWl	18.37 b	8.73 b	9.71 b	48.88 b	4.52 b	11.05 a	39.44 b	48.52 b	34.62 b	17.63	2.75 b	43.62 b	9.59 b
CWl	15.61 c	7.91 c	7.68 c	41.46 c	3.33 c	10.48 ab	36.53 c	44.02 c	31.41 c	18.14	2.42 c	42.54 b	9.62 ab
LSD (0.05)	1.75	0.28	1.00	2.74	0.48	0.68	1.02	2.53	2.31	-----	0.15	2.26	0.15
Genotype (G)	***	***	***	***	***	***	***	***	***	***	***	***	***
Ducula x1	19.21 bcdefg	11.77 a	7.69 fg	46.85 fghd	3.94 bcde	8.17 jk	41.62 bc	63.79 a	41.70 ab	21.65 a	2.97 bcde	46.10 cdef	11.00 b
Ducula x2	19.89 bcde	9.77 def	10.12 bcde	47.74 efgh	4.08 bcd	9.75 ghi	42.52 bc	47.15 bcd	39.72 bc	17.56 cdef	2.69 efghi	49.34 bc	8.38 gh
Ducula x3	20.90 b	10.10 cde	10.80 abc	49.11 efg	3.82 cde	9.83 fghi	54.40 a	47.31 bcd	39.59 bcd	17.86 cde	2.65 fghij	53.30 a	8.89 f
Ducula x4	20.22 bcd	10.45 bcd	9.77 bcde	47.75 efgh	3.89 bcde	9.42 hij	52.57 a	52.06 b	37.68 bcd	17.06 efgh	3.06 bcd	50.34 ab	9.12 ef
PRL/Sara	20.28 bc	11.51 a	8.77 ef	46.77 gh	3.34 e	8.92 ij	43.38 b	63.67 a	47.35 a	20.35 b	3.13 b	42.46 fghi	10.22 c
Vee/Myna	20.50 bcd	9.19 efg	11.31 ab	48.42 efgh	4.15 bcd	11.17 cdef	40.12 bcd	47.77 bc	36.32 bcd	17.30 defg	2.77 efghi	46.93 bcde	8.28 h
Et-13	17.84 gh	7.60 i	10.16 bcde	58.37 a	4.51 bc	13.33 a	28.89 f	41.81 d	23.79 f	15.56 i	2.60 ghij	45.47 def	9.03 ef
K6290-Bulk	17.12 h	7.96 hi	9.15 def	54.36 bc	5.31 a	10.17 efghi	41.08 bc	44.19 cd	39.40 bcd	18.53 c	2.38 j	40.21 i	8.97 f
K6295-4A	20.60 bc	8.36 ghi	12.24 a	51.04 cd	5.60 a	12.25 abc	41.16 bc	49.42 bc	37.20 bcd	16.04 hi	3.11 bc	40.76 hi	8.93 f
Israel	18.52 defgh	8.85 fgh	9.67 cde	50.61 cdef	5.55 a	10.75 defgh	35.11 de	46.40 bcd	29.00 ef	16.25 ghi	2.89 bcdefg	50.31 ab	9.68 d
HAR 1709	19.63 bcdef	8.83 fgh	10.80 abc	53.27 bcd	6.00 a	11.33 bcde	42.97 bc	50.06 b	40.18 b	17.85 cde	2.83 cdefgh	41.33 ghi	9.87 cd
HAR 1685	18.28 efgh	8.07 hi	10.21 bcde	47.41 efgh	4.26 bc	12.58 ab	33.12 ef	41.73 d	28.99 ef	16.60 fghi	2.53 ij	44.65 defg	9.47 de
HAR 710	19.14 cdefg	8.67 gh	10.47 bcd	49.64 defg	3.30 e	10.75 defgh	42.44 bc	47.35 bcd	39.41 bcd	18.34 cd	2.58 hij	42.83 fghi	11.81 a
HAR 604	23.48 a	11.43 ab	12.05 a	54.89 ab	3.83 cde	11.83 bcd	42.10 bc	59.27 a	32.82 de	17.12 efgh	3.48 a	48.29 bcd	11.00 b
HAR 1522	17.13 h	11.00 abc	6.13 g	42.20 i	3.52 de	7.50 k	53.55 a	60.77 a	42.07 ab	20.63 ab	2.94 bcdef	42.88 fghi	11.05 b
HAR 1407	18.03 fgh	8.60 gh	9.43 cde	45.04 hi	4.57 b	10.83 defg	38.34 cd	47.75 bc	32.97 cde	17.10 efgh	2.80 defghi	44.09 efghi	8.79 fg
LSD (0.05)	1.75	0.99	1.57	3.84	0.57	1.36	5.03	5.78	6.80	1.13	0.29	3.86	0.48
Wl X G	***	***	*	**	***	*	Ns	***	Ns	**	***	*	*
Mean	19.42	9.51	9.92	49.59	4.35	10.54	42.08	50.66	36.76	17.86	2.83	45.58	9.66
C.V. (%)	11.17	12.92	19.56	9.60	19.85	16.09	14.81	14.14	22.90	7.82	12.73	10.48	6.11

GYt=grain yield total; GYms=grain yield from main spikes; GYts=grain yield from tiller spikes; BYm=biomass yield at maturity; BYv= biomass yield (vegetative) at the end of treatment; PS= productive spikes; GPSa = grains per spike (average); GPms=grains per main spike; GPts=grains per tiller spike; SlPS=spikelets per spike; GPSl=grains per spikelet;KM=single kernel mass; SL=spike length; *,**,*** represent significance at 0.05, 0.01 and 0.001 probability levels, respectively. NS represent non-significance. Means followed by the same letter are not significantly different at 0.05 probability level. FD = free drainage; TWl = transient soil waterlogging stress; CWl = continuous soil waterlogging stress

Table 4.3. Mean effects of soil waterlogging stress x genotype interaction on grain yields and biomass yields of bread wheat, 1998

Genotype	GYt+			GYms			GYts			BYm			BYv		
	FD	TWI	CWI	FD	TWI	CWI	FD	TWI	CWI	FD	TWI	CWI	FD	TWI	CWI
	(g/pot)												(g/ 2 plants)		
Ducula x1	21.74	18.33	17.55	12.36	11.91	11.04	8.88	7.42	6.77	52.58	45.51	42.47	4.03	4.79	3.01
Ducula x2	22.47	19.97	17.22	11.10	9.35	8.85	11.37	10.62	8.38	52.85	48.24	42.15	4.33	4.03	3.88
Ducula x3	24.76	19.95	18.00	12.71	8.94	8.67	12.06	11.01	9.33	58.54	46.97	41.83	3.89	4.03	3.55
Ducula x4	23.68	18.85	18.13	12.75	9.11	9.49	10.93	9.74	8.65	54.62	45.91	42.73	4.06	4.52	3.07
PRL/Sara	23.84	19.18	17.82	13.69	11.16	9.67	10.14	8.02	8.15	54.70	42.50	43.10	4.11	3.31	2.60
Vee/Myna	23.95	19.73	17.83	10.77	8.79	8.02	13.18	10.94	9.81	56.12	47.38	41.77	4.46	4.41	3.59
Et-13	27.33	15.42	10.77	12.27	5.87	4.66	15.06	9.55	5.86	70.70	63.35	41.06	5.99	4.23	3.30
K6290-Bulk	26.00	14.18	11.17	11.48	6.79	5.64	14.52	7.39	5.53	66.79	55.23	41.07	7.18	5.70	3.05
K6295-4A	26.10	20.35	15.37	10.30	7.66	7.13	15.79	12.69	8.24	60.76	50.94	41.42	7.60	4.87	4.32
Israel	22.10	17.92	15.55	10.18	7.74	8.63	11.91	10.19	6.93	62.96	46.37	42.52	7.58	5.61	3.47
HAR 1709	23.52	18.33	17.04	10.39	7.82	8.30	13.14	10.51	8.74	62.44	51.67	45.69	7.15	6.46	4.39
HAR 1685	24.00	16.95	13.89	10.59	7.81	5.82	13.41	9.14	8.07	55.49	46.38	40.36	4.61	4.98	3.20
HAR 710	24.49	17.71	15.22	11.93	7.40	6.68	12.56	10.31	8.54	58.49	49.30	41.13	4.14	2.78	2.99
HAR 604	28.47	22.84	19.14	13.46	11.25	9.57	15.01	11.59	9.57	61.18	53.32	50.18	4.18	3.93	3.38
HAR 1522	22.26	17.05	12.09	14.89	10.34	7.77	7.37	6.71	4.33	51.90	42.88	31.81	4.66	3.17	2.78
HAR 1407	23.89	17.25	12.95	11.40	7.75	6.67	12.50	9.51	6.29	54.96	46.16	34.01	5.40	5.60	2.71
LSD (0.05)		3.03			1.72			2.71			6.66			1.21	

+See Table 4.2 for abbreviations.

Table 4.4. Mean effects of soil waterlogging stress x genotype interaction on components of yield of bread wheat, 1998

Genotype	PS+			GPms			SIPS			GPSI			GM			SLms		
	FD	TWI	CWI	FD	TWI	CWI	FD	TWI	CWI	FD	TWI	CWI	FD	TWI	CWI	FD	TWI	CWI
	(No.)												(g)			(cm)		
Ducula x1	8.75	8.25	7.50	68.13	63.88	59.38	19.94	22.44	22.58	3.45	2.83	2.62	44.54	44.32	49.45	10.57	11.54	10.91
Ducula x2	8.25	11.75	9.25	50.00	47.56	43.88	17.38	17.06	18.25	2.87	2.79	2.40	55.05	44.89	48.08	8.54	8.22	8.39
Ducula x3	7.75	10.50	11.25	52.13	44.25	45.56	17.77	17.44	18.38	2.92	2.54	2.48	60.34	50.14	49.42	8.94	9.22	8.51
Ducula x4	8.50	10.25	9.50	54.63	50.19	51.38	16.63	16.75	17.81	3.29	3.02	2.88	57.78	45.91	47.30	9.16	8.94	9.25
PRL/Sara	8.25	9.25	9.25	68.75	62.56	59.69	21.44	19.67	19.94	3.20	3.18	3.02	45.87	42.77	38.75	10.60	9.66	10.41
Vee/Myna	10.75	11.25	11.50	55.44	44.56	43.31	17.03	17.19	17.69	3.27	2.58	2.45	47.86	47.47	45.44	8.36	8.50	7.97
Et-13	14.50	14.25	11.25	67.44	31.81	26.19	18.06	14.75	13.88	3.75	2.17	1.89	48.89	44.37	43.15	9.63	8.85	8.63
K6290-Bulk	10.25	10.75	9.50	65.25	34.44	32.88	18.56	18.65	18.39	3.47	1.86	1.80	50.89	35.27	34.72	9.33	8.96	8.63
K6295-4A	12.50	12.25	12.00	55.38	47.31	45.56	14.94	16.13	17.06	3.71	2.94	2.67	45.88	37.42	38.98	8.32	9.16	9.32
Israel	12.25	10.50	9.50	50.63	45.38	43.19	15.56	15.88	17.31	3.27	2.89	2.50	53.59	48.69	48.65	9.60	9.50	9.93
HAR 1709	10.25	12.50	11.25	53.56	49.38	47.25	17.44	16.67	19.46	3.10	2.97	2.43	44.99	38.51	40.48	9.88	9.43	10.30
HAR 1685	11.50	12.25	14.00	51.13	41.50	32.56	15.88	16.94	17.00	3.22	2.45	1.92	51.72	43.74	39.18	9.38	9.41	9.63
HAR 710	9.75	11.25	11.25	62.06	39.88	33.25	18.65	17.75	18.63	3.34	2.49	1.93	47.64	40.86	37.85	12.23	11.32	11.88
HAR 604	11.50	11.50	12.50	62.25	61.25	54.31	16.88	17.61	16.88	3.68	3.48	3.26	53.17	50.91	40.78	11.22	10.86	10.91
HAR 1522	7.25	8.25	7.00	75.81	63.94	42.56	22.38	19.88	19.64	3.42	3.22	2.17	47.76	40.04	40.84	11.60	10.99	10.55
HAR 1407	9.25	12.00	11.25	58.38	44.00	40.88	16.69	17.25	17.38	3.50	2.55	2.35	53.47	42.34	36.46	8.71	8.87	8.78
LSD (0.05)		2.36			10.01			1.95			0.51			6.68			0.83	

+See Table 4.2 for abbreviations

Biomass yields

Biomass yields measured at maturity (BYm: g pot^{-1}) and after six weeks of waterloging (BYv: g per 2 plants) were significantly reduced with increased severity in waterlogging stress (Table 4.2). Relative to the control, TWl-treatment reduced BYm and BYv by 16.4 and 13.2% and CWl-treatment by 29.1 and 36.1%, respectively. Similar findings have been reported for waterlogged wheat in a clay soil (Cannell *et al.*, 1984) and alkaline and sodic soils (Sharma and Swarup, 1988, 1989; Gill *et al.*, 1993). The correlation between BYm and GYt was strong and positive under FD- and CWl-treatments (Tables 4.10 and 4.11). Musgrave and Ding (1998) found a strong positive correlation between biomass at maturity and grain yield for waterlogged winter wheat in a greenhouse pot experiment. Of the total variation in grain yield, 50.5% under FD- and 24.5% under CWl-treatment were resulted from BYm (Table 4.12). BYv also accounted for 2.4% of variation in grain yield under transient waterlogging conditions.

A significant difference among genotypes was detected for both BYm and BYv (Table 4.2). Heritability of BYm and BYv was 77.0 and 72.9%, respectively. Et-13 and HAR 604 had significantly the highest biomass yield at maturity and K6290-Bulk, K6295-4A, Israel and HAR 1709 had, significantly, the highest biomass yield when the waterlogging treatments ended. Waterlogging x genotype interaction was also significant for both BYm and BYv (Table 4.2). Differential biomass and shoot dry weight responses among wheat genotypes to waterlogging stress have already been documented elsewhere (Davies and Hillman, 1988; Huang *et al.*, 1994a, b, 1995; Musgrave and Ding, 1998). BYm was significantly reduced for all genotypes with increased severity in the waterlogging stress, but the magnitude of reduction was the

highest for Isreal, K6290-Bulk and Ducula x3 under transient waterlogging and for ET-13, K6290-Bulk, Israel, HAR 1522 and HAR 1407 under continuous waterlogging (Table 4.4). For the Ducula sister lines, BYv increased slightly under transient waterlogging; the other genotypes showed a progressive reduction in BYv with increased severity in the stress and the reduction was more pronounced on ET-13, K6290-Bulk, Israel and K6295-4A.

Yield components

Soil waterlogging stress had a significant effect on all the components of yield except on SlPS (Table 4.2). Increasing severity of waterlogging stress significantly reduced average number of grains per spike (GPSa) and number of grains per main spike (GPms), per tiller spike (GPts), per spikelet (GPSl) as well as kernel mass (KM: mg kernel^{-1}) and main plant spike length (SLms: cm). Relative to the FD-, the TWl-treatment reduced GPSa, GPms and GPts by 20.9, 18.4 and 21.8% and CWl-treatment by 26.8, 25.9 and 40.9%, respectively. The corresponding values for GPSl were 17.7 and 27. 5% and for KM were 13.8 and 15.9%. On the other hand, mean productive spikes (PS: no. Pot^{-1}) significantly increased (+9.6%) under transient waterlogging and the difference between the FD- and CWl- treatments were not significant, which is in agreement with findings reported by Watson *et al.* (1975) for Australian wheat cultivars and by Musgrave and Ding (1998) for wheat cultivars adapted to the Great Plains region in the USA. Similarly, the difference between TWl- and CWl- treatment effects on KM and SLms were not significant. GPms and GPts were positively correlated under stress conditions (Tables 4.10 and 4.11). GPms, KM, GPSl and SlPS correlated significantly and positively with GYt under waterlogging stress conditions. Productive spikes

correlated positively with GYt under FD- and CWl- condition. Therefore, in this study, grain yield depression under TWl- and CWl-treatments were largely attributed to a reduction in the number of grains per spike and to some extent to a decrease in individual kernel mass. This was confirmed by the stepwise regression analysis presented in Table 4.12. The results of stepwise regression indicated that under free drainage, PS, KM, GPSa and SlPS together accounted for a total of 26.2% and PS alone accounted for 19.1% of the variation in grain yield. Under transient waterlogging, PS, KM and GPSa together explained about 29.54% of the variation in the grain yield and GPSa alone accounted for 23.6% of the variability in grain yield. Under continuous waterlogging, GPSa, SlPS, KM and PS together accounted for 20.1% of the variation in grain yield. These results are in agreement with the findings of Musgrave and Ding (1998) who concluded that a 45% decrease in grain yield of winter wheat due to prolonged waterlogging in greenhouse pot experiment was attributed to a 45% decrease in the number of kernels per spike and a 5% decrease in kernel weight. In contrast to this conclusion, Cannell *et al.* (1984) from a lysimeter study and Sharma and Swarup (1988; 1989) from the field study showed that grain yield reduction in wheat due to waterlogging stress resulted rather from a decline in the number of fertile tillers than number of grains per spike or 1000-kernel weight.

Genotypic differences were significant for all the yield components of bread wheat (Table 4.2). Heritability values of 92.3, 85.3 and 77.3% were calculated for GPSa, PSm and KM, respectively. Ducula x3 and x4, and HAR 1522 had the highest number of GPSa in this study. Ducula x1, PRL/Sara, HAR 604 and HAR 1522 had significantly higher number of GPms and GPts than other genotypes studied. Et-13 followed by HAR

1685 had the lowest number of GPSa, GPms, GPts and SIPS. ET-13 and HAR 1685 followed by K6295-4A had, significantly, the highest number of productive spikes per pot. Individual kernel mass was significantly the heaviest for Ducula x3, Ducula x4 and Israel followed by Ducula x2 and HAR 604, and the lightest for K6290-Bulk and K6295-4A. HAR 710 followed by HAR 604, HAR 1522 and Ducula x1 had significantly longer main plant spikes and K6290-Bulk, K6295-4A, Ducula x3 and HAR 1407 had the shortest spikes of all the genotypes studied.

A significant waterlogging stress x genotype interaction was detected for PS, GPms, SIPS, GPSl, KM and SLms (Table 4.2). With increasing waterlogging stress, PS was significantly decreased for ET-13 and Israel and increased for Ducula x3 and HAR 1685 (Table 4.4). Significant reductions in mean GPms and KM was evident for most genotypes as severity in stress increased, but the degree of reduction in these components depended on genotypes. A decrease in GPms was more pronounced on Et-13, K6290-Bulk, K6295-4A, HAR 1685, HAR 710, HAR 1522 and HAR 1407. The decreases in KM were more pronounced on K6290-Bulk, HAR 1685 and HAR 1407 than on other genotypes. Transient waterlogging reduced the mean KM significantly for Ducula x2, Ducula x4, K6295-4A and HAR 1522. Differential yield component responses of wheat genotypes to waterlogging stress was also reported by van Ginkel *et al.* (1992), Gill *et al.* (1993), Gardner and Flood (1993), Huang *et al.* (1994).

Plant height

Both plant height measures (PHv and PHm) and shoot elongation rate (SER) were significantly decreased with increased severity in waterlogging stress (Table 4.5).

During the six weeks of waterlogging, mean shoot elongation rate of the genotypes under transient and continuous waterlogging was significantly retarded by 9.8 and 29.5% compared to the freely drained control. At the end waterlogging period, the plants of the TWl- and CWl- treatments were respectively five and 11 cm shorter than those of freely drained, and this effect lasted till to maturity. In India, Gill *et al.* (1993) reported a significant decrease in the height of wheat plant with increased level of flooding on an alkaline soil.

Genotypes showed significant differences for all height measurements and SER. Heritabilities of PHs, PHv, PHm and SER were 97.8, 88.9, 83.1 and 94.2%, respectively. When the waterlogging started, ET-13 and K6290-Bulk were the tallest genotypes followed by K6295-4A, whereas HAR 1522 was the shortest genotype. After six weeks of waterlogging, K6295-4A and HAR 1709 were the tallest and HAR 604 was the shortest genotype. At maturity, K6290-Bulk, K6295-4A, Israel and HAR 1709 had the highest and HAR 1685 the lowest height in the study. K6295-4A and HAR 1709 had the fastest and HAR 604 the slowest SER. The interactions between waterlogging and genotype were significant for PHv, PHm and SER (Tables 4.5 and 4.6). Both stress treatments significantly reduced plant height and inhibited SER; the effects were more pronounced on Et-13, K6290-Bulk, Israel and HAR 1709. Similar findings were reported by Gill *et al.* (1993) under field condition. PHv accounted for 8.55% of variation in grain yield under the FD-treatment condition (Table 4.12).

Table 4.5. Statistical significance and mean effects of treatments on plant height, shoot elongation rate, number of green leaf and heading and maturity of bread wheat genotypes, 1998

Factor	PHs+	PHv	PHm	SER	DH	DPM	Green leaves per four main plants (GLN)				
		(cm)		(cm/day)	(days)		2-wk	3-wk	4-wk	5-wk	6-wk
							(no.)				
Heritability (h^2_b)	97.83	88.92	83.12	94.15	95.87	92.10	73.26	79.58	74.92	78.32	92.73
Waterlogging (WI)	-----	***	***	***	***	***	**	***	***	**	***
FD	-----	57.05 a	99.57 a	0.937 a	74.41 c	142	17.16 a	21.97 a	18.20 a	15.78 a	11.88 a
TWI	-----	52.01 b	92.48 b	0.845 b	80.48 b	147	15.50 b	18.63 b	14.59 b	14.14 b	9.13 b
CWI	-----	46.09 c	87.21 c	0.661 c	84.56 a	151	15.69 b	16.23 c	13.67 b	12.60 c	8.84 b
LSD (0.05)	-----	2.32	3.38	0.05	1.98	2.51	0.79	1.09	1.11	1.09	0.57
Genotype (G)	***	***	***	***	***	***	***	***	***	***	***
Ducula x1	18.67fg	43.89 ef	90.09 efg	0.662 de	95.42 b	158 b	17.08 abc	21.25 a	17.08 a	15.92 a	11.58 a
Ducula x2	19.03ef	44.56 ef	90.56 efg	0.670 de	81.75 de	146 def	15.75 efg	18.83 bcde	15.08 defg	14.25 bcd	9.75 de
Ducula x3	18.78fg	46.51 ef	90.47 efg	0.732 d	83.25 d	146 def	15.17 fg	17.00 f	14.58 g	13.67 d	10.17 cd
Ducula x4	19.39de	47.24 e	90.92 ef	0.734 d	88.83 c	154 c	15.83 defg	18.42 cdef	15.67 cdef	14.00 bcd	10.08 cd
PRL/Sara	18.24g	43.99 ef	94.88 cde	0.700 d	87.42 c	149 d	16.08 cdef	17.67 ef	15.75 bcde	14.42 bcd	10.75 bc
Vee/Myna	18.7fg	44.06 ef	89.02 efg	0.675 de	80.50 e	145 efg	16.00 defg	17.67 ef	14.92 efg	13.58 d	10.08 cd
Et-13	21.27a	54.45 d	97.87 bcd	0.851 c	102.0 a	166 a	18.00 a	19.58 bcd	15.08 defg	13.67 d	9.67 de
K6290-Bulk	21.80a	62.50 c	104.5 ab	0.900 c	73.42 g	139 jk	16.58 bcde	19.67 abcd	14.58 g	12.08 e	7.42 g
K6295-4A	20.52b	67.69 a	99.23 abc	1.181 a	67.17 i	140 hij	15.67 efg	19.25 bcde	15.50 cdefg	13.83 d	9.08 ef
Israel	19.95c	63.99 bc	105.4 a	0.990 b	68.17 hi	143 ghi	17.58 ab	21.25 a	16.42 abc	15.08 ab	9.83 d
HAR 1709	19.79cd	67.36 ab	103.2 ab	1.142 a	67.00 i	140 ij	14.83 g	17.83 ef	14.67 fg	13.92 cd	8.92 f
HAR 1685	19.84cd	47.14 e	77.82 h	0.677 de	67.50 i	135 k	15.33 fg	17.67 ef	15.25 defg	14.67 bcd	10.67 bc
HAR 710	18.57fg	44.46 ef	91.24 def	0.675 de	79.83 e	142 ghi	17.00 abcd	20.33 ab	16.00 bcd	13.58 bcd	10.92 ab
HAR 604	18.66fg	43.18 f	93.72 cde	0.612 e	87.83 c	153 c	15.67 efg	19.75 abc	16.75 ab	15.00 abc	10.92 ab
HAR 1522	16.31h	53.43 d	83.85 gh	0.926 bc	76.42 f	149 de	15.08 fg	18.08 def	15.17 defg	14.00 bcd	9.83 d
HAR 1407	18.72fg	53.03 d	86.63 fg	0.900 c	70.58 h	143 fgh	16.17 cdef	18.83 bcde	15.33 defg	14.17 bcd	9.50 def
LSD (0.05)	0.55	3.47	6.71	0.08	2.51	3.59	1.21	1.62	1.06	1.09	0.74
W X G	------	***	*	***	***	***	Ns	**	***	***	***
Mean	19.26	51.72	93.09	0.814	79.82	146.68	16.12	18.94	15.49	14.18	9.95
C.V. (%)	2.00	8.30	8.93	11.73	3.96	3.03	9.33	10.62	8.44	9.52	9.18

+PHs = Plant height (seedling) at the start of treatments; PHv = plant height (vegetative) at the end of treatment; PHm = plant height at maturity; SER = shoot elongation rate; DH = days to heading; DPH = days to physiological maturity; wk = week; *,**,*** represent significance at 0.05, 0.01 and 0.001 probability levels, respectively. NS represent non-significance. Means followed by the same letter are not significantly different at 0.05 probability level.

Table 4.6. Mean effects of soil waterlogging stress x genotype interaction on plant height, shoot elongation rate, and days to heading and maturity of bread wheat genotypes, 1998

Genotype	PHv+			PHm			SER			DH			DPM		
	FD	TWl	CWl	FD	TWl	CWl	FD	TWl	CWl	FD	TWl	CWl	FD	TWl	CW
	(cm)						(cm/day)			(days)					
Ducula x1	46.50	44.80	40.38	93.10	89.44	87.75	0.732	0.688	0.566	88	97	102	151	157	167
Ducula x2	44.84	46.53	42.31	93.50	92.81	85.36	0.698	0.713	0.600	81	82	83	145	146	148
Ducula x3	49.35	46.85	43.34	95.86	88.63	86.94	0.829	0.753	0.613	80	84	86	146	146	147
Ducula x4	48.10	49.25	44.38	93.69	90.88	88.19	0.768	0.805	0.630	87	88	92	152	155	154
PRL/Sara	47.70	44.86	39.41	103.94	94.19	86.50	0.804	0.738	0.558	84	88	91	147	149	151
Vee/Myna	45.70	46.64	39.84	89.31	92.50	85.25	0.750	0.755	0.519	73	83	87	141	146	150
Et-13	62.28	54.16	46.90	108.22	94.81	90.63	1.071	0.852	0.630	84	106	116	151	167	180
K6290-Bulk	79.15	61.31	47.03	112.94	110.31	90.17	1.137	0.939	0.624	67	73	81	132	138	146
K6295-4A	71.68	68.30	63.10	106.25	100.00	91.44	1.276	1.211	1.056	63	68	71	135	138	146
Israel	84.68	57.98	49.33	117.94	102.50	95.69	1.285	0.945	0.740	61	69	75	138	145	145
HAR 1709	73.83	66.20	62.06	125.25	89.18	95.25	1.303	1.146	0.978	61	69	72	135	139	145
HAR 1685	51.80	48.63	40.99	83.38	77.71	72.38	0.782	0.731	0.519	63	66	72	133	136	137
HAR 710	48.24	43.29	41.85	96.33	91.44	85.94	0.779	0.654	0.593	77	82	81	135	145	147
HAR 604	46.35	43.25	39.93	94.94	96.58	89.63	0.758	0.659	0.419	84	89	91	149	152	158
HAR 1522	59.95	53.31	47.04	89.38	81.00	81.19	1.095	0.922	0.761	71	79	80	143	152	151
HAR 1407	52.63	56.86	49.60	89.19	87.63	83.06	0.927	1.006	0.766	69	68	75	144	140	147
LSD (0.05)		6.00			11.62			0.133			4.42			6.22	

+See Table 4.5 for abbreviations

Heading and maturity

Continuous waterlogging significantly delayed both heading and maturity more than transient waterlogging, which in turn took longer than the freely drained control (Table 4.5). On average, wheat genotypes under TWl- and CWl- treatment took respectively about six and 10 days longer to reach heading. On alkaline and sodic soils in India, Sharma and Swarup (1988, 1989) noted a significant delay in days to heading and maturity of wheat due to short-term (6 days) waterlogging. Et-13 followed by Ducula x1 took the longest to reach heading; where as HAR 1685, HAR 710, HAR 1709 and K6295-4A were significantly faster. Heritabilities of DH and DPM were quite high, 95.9 and 92.1%, respectively (Table 4.5). With increased severity in waterlogging stress, HD was significantly delayed for most genotypes, but the delay was most marked in Et-13 followed by Ducula x1, Vee/Myna, K6290-Bulk, Israel and HAR 1709 (Table 4.6). The effect on maturity also followed a similar trend as HD. In a pot experiment, Watson *et al.* (1976) also reported that 42 days of intermittent or continuous waterlogging significantly delayed ear emergence of wheat, barley and oats, but the delay was most pronounced in wheat. Gardner and Flood (1993) reported that waterlogging effects were significantly higher on early than on later maturing wheat genotypes and suggested that late maturing genotypes tolerate waterlogging stress better than early maturing types. In this study, however, DH did not correlate with GYt (Tables 4.10 and 4.11). Boru (1996) also reported similar results. In the stepwise regression, DH was indicated as an important independent characteristic only under TWl-treatment condition, accounting for 6.6% of the total variation in grain yield (Table 4.12).

Table 4.7. Mean effects of soil waterlogging stress x genotype interaction on the number of green leaves in bread wheat genotypes, 1998

Genotypes	Number of green leaves from four main plants (no.)											
	3-wk			4-wk			5-wk			6-wk		
	FD	TWI	CWI	FD	TWI	CWI	FD	TWI	CWI	FD	TWI	CWI
Ducula x1	24.00	20.50	19.25	19.00	16.00	16.25	17.25	15.75	14.75	12.50	10.50	11.75
Ducula x2	21.00	19.75	15.75	16.25	14.75	14.25	14.75	14.00	14.00	11.25	9.25	8.75
Ducula x3	20.00	17.75	13.25	17.25	14.25	12.25	14.75	13.50	12.75	11.50	9.25	9.75
Ducula x4	20.50	18.25	16.50	16.50	15.50	15.00	15.50	14.00	12.50	11.25	9.25	9.75
PRL/Sara	20.00	17.00	16.00	18.25	14.00	15.00	15.50	14.00	13.75	11.75	10.75	9.75
Vee/Myna	19.50	19.50	14.00	16.75	15.75	12.25	14.50	14.00	12.25	11.75	9.00	9.50
Et-13	22.00	19.00	17.75	19.50	13.75	12.00	17.50	13.50	9.75	14.00	7.75	7.25
K6290-Bulk	24.00	21.50	13.50	18.25	13.25	12.25	16.00	12.50	7.75	11.75	5.50	5.00
K6295-4A	23.00	17.75	17.00	19.25	14.25	13.00	15.50	14.50	11.50	10.75	8.75	7.75
Israel	24.00	20.25	19.50	19.50	15.25	14.50	15.75	14.50	15.00	12.25	9.00	8.25
HAR 1709	20.00	17.50	16.00	17.50	13.50	13.00	15.50	13.50	12.75	11.00	8.00	7.75
HAR 1685	20.00	18.75	14.25	17.75	14.75	13.25	16.00	14.25	13.75	12.50	10.00	9.50
HAR 710	24.00	18.00	19.00	18.25	14.50	14.25	15.25	15.00	13.50	12.25	10.25	10.25
HAR 604	23.00	18.50	17.75	19.50	16.00	14.75	16.50	15.00	13.50	12.50	10.00	10.25
HAR 1522	22.50	17.00	14.75	18.75	14.00	12.75	16.25	13.75	12.25	12.00	9.50	8.00
HAR 1407	24.00	17.00	15.50	19.00	14.00	13.00	15.75	14.50	12.25	11.00	9.25	8.25
LSD (0.05)		2.81			1.83			1.89			1.28	

[+]See Table 4.5 for abbreviations

Leaf count

The numbers of green leaves per main plants, which were counted on five occasions during the six weeks of waterlogging, were significantly affected by waterlogging stress and genotypic differences (Table 4.5). Transient waterlogging significantly reduced the number of green leaves (GLN) in all counts. Transient waterlogging resulted in a further significant reduction with the second and fourth counts. Ducula x1 and HAR 604 showed consistently the highest GLN on main plants and K6290-Bulk had the lowest GLN with the last three counts. Heritabilities of GLN ranged from 73.3 to 92.7. Waterlogging x genotype interaction effects on GLN were significant for all except for the first count (Table 4.5 and 4.7). The adverse effects of waterlogging on GLN for most genotypes became increasingly serious with later counts. Et-13 and K6290-Bulk showed the greatest reduction in GLN under both transient and continuous waterlogging than most other genotypes, especially PRL/Sara, Ducula x1 and HAR 604. The GLN at heading (fifth count) correlated significantly and positively with GYt and GPms in all three treatments (Tables 4.10 and 4.11). He *et al.* (1993) working on wet-stress resistance reported that the green leaf number on main plants to be the second most important characteristic contributing towards wet-stress resistance in barley, but not in wheat. Other workers (Cai and Cao, 1991; Cai *et al.*, 1994a; Cao *et al.*, 1994; Cao *et al.*, 1995) have, however, used the number of green leaves on main plants as criterion to select wheat genotypes tolerant to waterlogging stress. From the results reported herein, it is clear that the number of green leaves at heading is a good indicator of the tolerance of wheat genotypes to waterlogging stress.

Leaf chlorosis

Leaf chlorosis and premature senescence of the older leaves are characteristic symptoms of waterlogging damage on wheat plants (Drew and Sisworo, 1977; Belford, 1981; Cannell *et al.*, 1980). In this study, desiccation of succulent young leaves and wilting and rolling of older leaves appeared after one week of waterlogging, apparently indicating internal water stress, especially on the most sensitive genotypes. A week later, these symptoms were apparent on most other genotypes, and was preceded by leaf tip yellowing followed by yellowing and drying of the older leaves on the shoots, suggesting that nutrient uptake may have been restricted and, hence, attributed to waterlogging damage (Trought and Drew, 1980a).

Soil waterlogging had a significant effect on the percentage leaf chlorosis (Chl) score (except on the first score) and the area under chlorosis progress curve (AUCPC) (Table 4.8). Continuous waterlogging resulted in a higher percentage leaf Chl score and AUCPC-values than transient waterlogging, the effect was more marked with the later scorings. In a lysimeter study, Cannell *et al* (1980) also observed a more pronounced leaf chlorosis and early senescence of older leaves on wheat plants waterlogged for three weeks than those on freely drained soil. Wheat genotypes differed significantly at all the Chl scores and AUCPC-values (Table 4.8). Heritability was 90.5 for AUCPC-value and ranged from 81.7 to 90.8% for percentage Chlorosis scored at the different occasions. Et-13 and K6290-Bulk had the highest and PRL/Sara, Ducula x1, Ducula x4 and HAR 604 exhibited the lowest mean percent leaf Chl and AUCPC-values in this study (Table 4.8 and Fig. 4.2). The low leaf chlorosis and AUCPC-values obtained on CIMMYT lines in this study is in agreement with the findings of Van Ginkel *et al.*

(1992) reported for the same lines under prolonged waterlogging in the field conditions in Mexico. Boru (1996) also found the lowest leaf chlorosis of 18% and an AUCPC-value of 341 on F3's from a cross of tolerant parents (Ducula x Verry/Myna) and the highest values of 70% and 1382, respectively, on F_3 populations from susceptible parent crosses (Seri-82 and Kite/Glen). In a similar study involving synthetic hexaploid wheats, Villareal and Mujeeb-Kazi (1999) reported a mean leaf chlorosis of 43% with values ranging from 7 to 75% and found five synthetic entries with a mean percentage chlorosis less than 10%.

The effect of the level of soil waterlogging stress on percentage Chl (on three of the five scores) and AUCPC-values depended on genotypes, as indicated by a significant waterlogging x genotype interaction (Table 4.8). Percentage Chl and AUCPC-values for all genotypes were greater for the CWl- treatment than for the TWl- treatment, but the magnitudes were less marked on PRL/Sara, Ducula x1 and HAR 604 but highly pronounced on K6290-Bulk, Et-13, Israel, HAR 1522 and HAR 1407. Van Ginkel *et al.* (1992) and Boru (1996) also recorded less leaf chlorosis and AUCPC-values for PRL/Sara, Vee/Myna and Ducula after six weeks of waterlogging under field conditions.

Table 4.8. Statistical significance and mean effects of treatments on stress indices and leaf chlorosis of bread wheat genotypes, 1998

Factor	Stress indices		Leaf chlorosis score (Chl)					AUCPC
	SSI+	STI	2-wk+	3-wk	4-wk	5-wk	6-wk	
			(%)					
Heritability (h^2_b)	95.08	92.16	90.78	81.68	84.96	85.41	88.18	90.45
Waterlogging (WI)	Ns	**	Ns	***	*	***	*	***
TWI	0.966	1.187	6.81	12.80	21.52	27.14	36.33	581.16
CWI	0.970	1.003	8.01	21.09	30.19	40.06	47.03	832.07
Genotype (G)	***	***	***	***	***	***	***	***
Ducula x1	0.576 f	1.042 cdef	2.50 e	10.13 c	19.38 fgh	22.13i	26.25 i	462.00i
Ducula x2	0.523 f	1.104 bcde	2.75 e	13.50 c	22.25 efg	24.88ij	29.38 hi	536.81hi
Ducula x3	0.777 cdef	1.249 b	8.38 bc	16.00 bc	24.63 de	27.88hi	33.13 gh	624.75gh
Ducula x4	0.726 ef	1.158 bcd	2.75 e	12.75 c	21.75 efg	24.75ij	25.00 i	511.88i
PRL/Sara	0.755 def	1.174 bc	3.63 de	12.88 c	16.25 h	24.75ij	25.00 i	477.31i
Vee/Myna	0.699 ef	1.196 bc	2.00 e	12.63 c	19.38 fgh	26.63i	38.75 fg	553.00hi
Et-13	1.738 a	0.952 ef	15.13 a	24.13 a	36.13 ab	47.63b	57.50 b	1009.31b
K6290-Bulk	1.721 a	0.873 f	7.38 bcd	16.75 bc	39.38 a	60.00a	76.88 a	1107.75a
K6295-4A	1.027 bcde	1.238 b	14.75 a	26.00 a	30.63 c	37.88cde	45.00 de	870.63c
Israel	0.781 cdef	0.980 def	5.63 cde	16.63 bc	28.75 cd	34.38efg	50.63 cd	755.13def
HAR 1709	0.802 cdef	1.108 bcde	11.88 ab	16.63 bc	32.50 bc	36.25def	44.38 ef	794.50cde
HAR 1685	1.179 b	0.984 def	8.88 bc	16.75 bc	22.50 efg	33.75fg	45.63 de	701.75efg
HAR 710	1.096 bcd	1.068 bcde	7.38 bcd	14.88 bc	24.13 def	31.25gh	41.88 ef	664.125fg
HAR 604	0.859 bcdef	1.583 a	8.00 bcd	15.00 bc	18.50 gh	25.50ij	29.38 hi	543.813hi
HAR 1522	1.102 bcd	0.860 f	9.75 bc	24.88 a	29.00 cd	38.38cd	45.00 de	837.38cd
HAR 1407	1.128 bcd	0.952 ef	7.88 bcd	21.63 ab	28.50 cd	41.63c	53.13 bc	855.75c
LSD (0.05)	0.361	0.183	4.51	7.11	5.01	3.86	6.04	92.86
W X G	Ns	Ns	Ns	Ns	*	***	***	***
Mean	0.968	1.095	7.414	16.95	25.85	33.60	41.68	706.62
C.V. (%)	37.47	16.74	61.22	42.21	19.51	11.55	14.59	13.23

+ wk= week; SSI = stress sensitivity index; STI = stress tolerance index; AUCPC = area under chlorosis curve; *,**,*** represent significance at 0.05, 0.01 and 0.001 probability levels, respectively. NS represent non-significance. Means followed by the same letter are not significantly different at 0.05 probability level

Table 4.9. Mean effects of soil waterlogging stress x genotypes on percentage leaf chlorosis in bread wheat, 1998

Genotype	Leaf chlorosis score							
	4-wk		5-wk		6-wk		AUCPC	
	TWI	CWI	TWI	CWI	TWI	CWI	TWI	CWI
	(%)							
Ducula x1	17.00	21.75	19.50	24.75	25.00	27.50	406.88	517.13
Ducula x2	19.50	25.00	19.75	30.00	27.50	31.25	420.00	653.63
Ducula x3	17.50	31.75	20.75	35.00	30.00	36.25	458.50	791.00
Ducula x4	16.75	26.75	20.75	28.75	22.50	27.50	394.63	629.13
PRL/Sara	12.50	20.00	22.00	27.50	21.25	28.75	412.13	542.50
Vee/Myna	12.00	26.75	20.75	32.50	33.75	43.75	397.25	708.75
Et-13	25.50	46.75	31.50	63.75	38.75	76.25	738.50	1280.13
K6290-Bulk	36.25	42.50	50.00	70.00	65.00	88.75	906.50	1309.00
K6295-4A	25.00	36.25	30.75	45.00	43.75	46.25	742.88	998.375
Israel	26.25	31.25	23.75	45.00	40.00	61.25	602.00	908.25
HAR 1709	31.25	33.75	28.75	43.75	43.75	45.00	706.13	882.88
HAR 1685	17.50	27.50	32.50	35.00	41.25	50.00	591.50	812.00
HAR 710	20.75	27.50	30.00	32.50	37.50	46.25	640.50	687.75
HAR 604	18.25	18.75	19.75	31.25	26.25	32.50	466.38	621.25
HAR 1522	23.75	34.25	30.50	46.25	37.50	52.50	682.50	992.25
HAR 1407	24.50	32.50	33.25	50.00	47.50	58.75	732.38	979.13
LSD (0.05)	7.09		5.43		8.54		131.3	

[+]See table 4.8 for abbreviations

Degree of leaf chlorosis has been used as the principal selection criterion in wheat for tolerance to waterlogging stress (Van Ginkel *et al.*, 1992; Boru, 1996; Villareal and Mujeeb-Kanzi, 1999). In this study, both percentage chlorosis at heading and the AUCPC-values correlated negatively with GYt, GYms, KM and GLN under both stress conditions (Table 4.11). In similar studies conducted under field conditions, van Ginkel *et al.* (1992) and Boru (1996) reported significant negative phenotypic correlations between percentage leaf chlorosis at heading and final grain yield and between AUCPC-values and final grain yield. In another study comparing different synthetic hexaploid wheat genotypes under waterlogged field conditions, Villareal and Mujeeb-Kenzi (1999) reported significant negative phenotypic correlations for the association of percentage leaf chlorosis with yield per spike, number of grains per spike, 1000-kernel weight, grain filling period, plant height and spike length. They also noted significant positive associations between leaf chlorosis and days to heading and physiological maturity. In this study, however, a significant positive correlation was observed only for the association of the percentage Chl with BYv, PHv and SER under TWI treatment and for AUCPC-value with PHv and SER under both stress treatment conditions. Regression analysis (Table 4.12) showed that Chlorosis was the single most important yield determinant under waterlogging conditions and that respectively 34.0 and 48.7% of the variation in grain yield under transient and continuous waterlogging conditions were explained by the percentage leaf chlorosis.

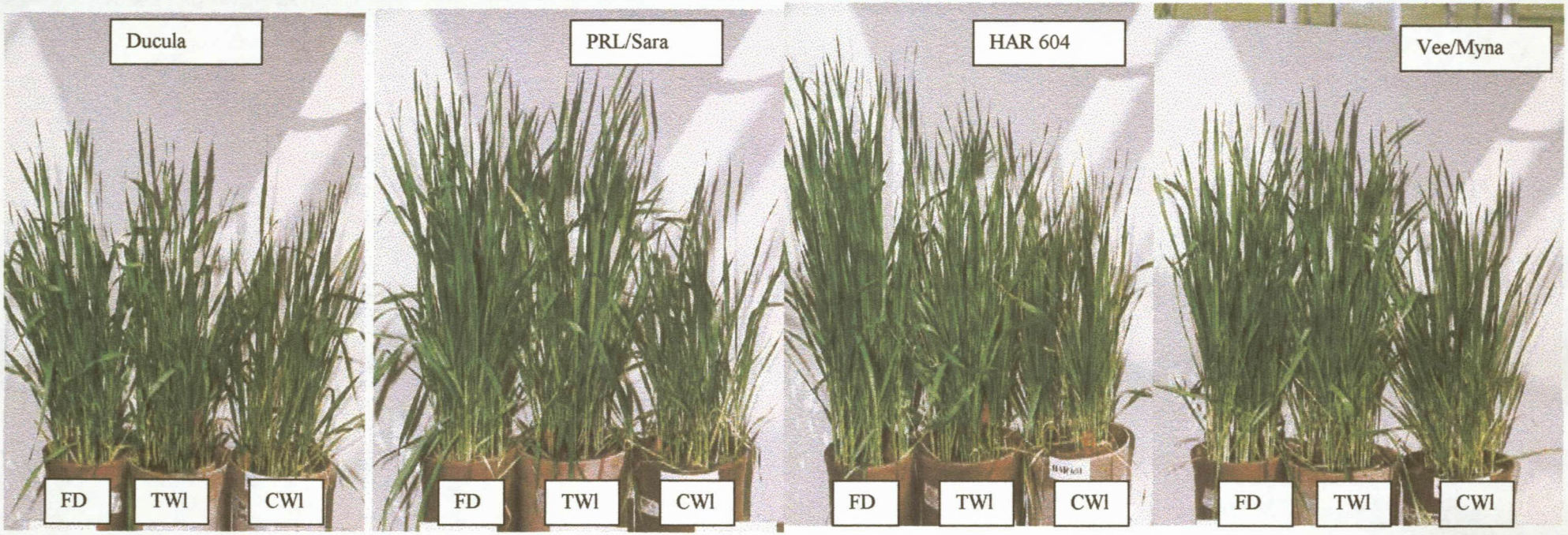

Figure 4.2. Pictures showing the reaction of tolerant genotypes to different levels of waterlogging after one month of treatment application (FD= free drainage; TWl=transient waterlogging; CWl=continuous waterlogging)

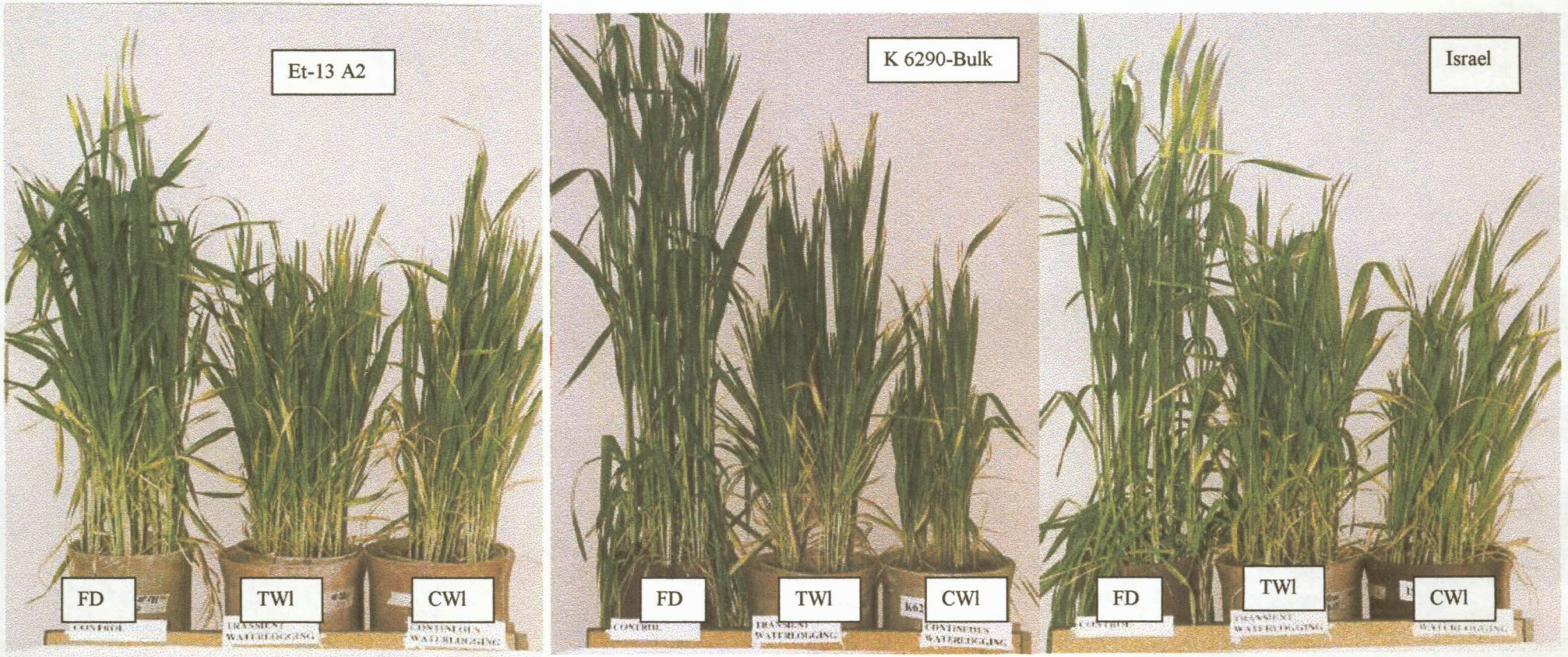

Figure 4.3. Pictures showing the reaction of sensitive genotypes to different levels of waterlogging after one month treatment application (FD= free drainage; TWl=transient waterlogging; CWl=continuous waterlogging)

Sensitivity Index

The yield-based stress sensitivity index (SSI) and stress tolerance index (STI) calculated for each of the 16 genotypes are presented in Table 4.8. The level of waterlogging treatment was only significantly different for STI. Genotypes, showed, had a significant difference for both SSI- and STI- values. The mean SSI- and STI- values were 0.966 and 1.187 for the TWl- and 0.970 and 1.003 for the CWl-treatments, respectively. Heritability was 95% for SSI-values and 92% for STI-values. Et-13 and K6290-Bulk followed by HAR 1685 showed the highest and the six CIMMYT lines had the lowest SSI-values. The STI-values were the highest for HAR 604 and lowest for K6290-Bulk, HAR1522, Et-13 and HAR 1407. Values >1 for STI and <1 for SSI-values indicates good level of tolerance to imposed stress, where as values <1 for STI-values and >1 for SSI-values indicates high susceptibility (Fischer and Maurer, 1998; Fernandez, 1992). There was no significant waterlogging x genotype interaction for both indices, indicating that genotypes used in this study do not differ greatly in stress susceptibility or tolerance when grown either unde transient or continuous waterlogging. This was supported by a significant correlation between the grain yields of the TWl- and CWl-treatments (r = 0.569***). Significant negative correlations were detected for the association of SSI-values with GPms, SlPS, GPSl, and GLN under both waterlogging treatments and with KM and BYm under CWl-treatment conditions (Table 4.11). Significant positive correlations were found for the association of STI-values with GPSl, GM and BYm under both waterlogging treatments and with PS, GPms and GLN under CWl-treatment.

Table 4.10. Correlation coefficients of characteristics of wheat genotypes grown on freely drained soil, 1998

Characteristic+	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1. GYt	0.254 *	0.801 *	0.474 ***	0.049 ns	0.255 *	0.041 ns	-0.003 ns	0.341 **	0.087 ns	0.009 ns	0.713 ***	0.017 ns	0.139 ns	0.035 ns	0.015 ns	0.393 **	-0.054 ns
2. GYms		-0.370 **	-0.411 ***	0.628 ***	0.653 ***	0.347 **	0.666 ***	0.166 ns	0.576 ***	0.064 ns	-0.049 ns	-0.390 **	-0.131 ns	-0.343 **	0.427 ***	-0.198 ns	-0.256 *
3. GYts			0.704 ***	-0.331 **	-0.160 ns	-0.164 ns	-0.418 ***	0.228 ns	-0.276 *	-0.032 ns	0.713 ***	0.262 *	0.217 ns	0.250 *	0.179 ns	0.181 ns	-0.319 *
4. PSm				-0.659 ***	-0.011 ns	-0.670 ***	-0.404 **	0.443 ***	-0.171 ns	-0.294 *	0.616 ***	0.394 **	0.272 *	0.344 **	0.264 *	0.279 *	-0.269 *
5. GPSa					0.566 ***	0.855 ***	0.710 ***	-0.009 ns	0.457 ***	-0.279 *	0.178 ns	-0.354 **	-0.050 ns	-0.277 *	-0.183 ns	-0.135 ns	0.236 ns
6. GPms						0.123 ns	0.705 ***	0.610 ***	0.556 ***	-0.542 ***	0.164 ns	-0.179 ns	0.088 ns	-0.123 ns	-0.079 ns	0.329 **	0.268 *
7. GPts							0.418 ***	-0.309 *	0.209 ns	-0.033 ns	-0.152 ns	-0.301 *	-0.047 ns	-0.221 ns	-0.130 ns	-0.104 ns	0.161 ns
8. SlPS								-0.125 ns	0.620 ***	-0.269 *	-0.039 ns	-0.311 *	0.055 ns	-0.233 ns	-0.160 ns	0.231 ns	0.340 **
9. GPSl									0.086 ns	-0.471 ***	0.250 *	0.112 ns	0.059 ns	0.087 ns	0.073 ns	0.190 ns	-0.009 ns
10. SLms										-0.266 *	0.055 ns	-0.294 *	0.042 ns	-0.151 ns	-0.102 ns	0.318 *	0.256 *
11.GMa											-0.097 ns	-0.120 ns	-0.255 *	-0.095 ns	-0.113 ns	-.028 ns	0.073 ns
12.BYm												0.369 **	0.512 ***	0.421 ***	0.337 **	0.325 *	-0.187 ns
13.BYv													0.580 ***	0.762 ***	0.696 ***	-0.047 ns	-0.599 ***
14.PHm														0.548 ***	0.507 ***	0.100 ns	-0.191 ns
15.PHv															0.920 ***	0.010 ns	-0.624 ***
16.SER																-0.037 ns	-0.553 ***
17.GLN5																	0.092 ns
18.DH																	

+See Tables 4.2, 4.5 and 4.8 for abbreviations

Table 4.11. Correlation coefficients of characteristics of wheat genotypes grown under transient (upper diagonal) and continuous waterlogging (lower diagonal) treatments, 1998

Characteristic*	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
1. GYt		0.581 ***	0.758 ***	0.057 ns	0.243 ns	0.401 **	0.104 ns	0.111 ns	0.422 ***	0.177 ns	0.405 **	0.138 ns	-0.105 ns	0.042 ns	-0.232 ns	-0.176 ns	0.337 **	0.016 ns	-0.485 ***	-0.583 ***	-0.681 ***	0.842 ***
2. GYms	0.762 ***		-0.064 ns	-0.506 ***	0.642 ***	0.791 ***	0.299 *	0.631 ***	0.562 ***	0.467 ***	0.322 *	-0.307 *	-0.298 *	-0.146 ns	-0.424 ***	-0.354 **	0.521 ***	0.219 ns	-0.570 ***	-0.608 ***	-0.561 *	0.383 **
3. GYts	0.814 ***	0.248 ns		0.487 ***	-0.206 ns	-0.127 ns	-0.102 ns	-0.315 *	0.048 ns	-0.117 ns	0.202 ns	0.420 ***	0.144 ns	0.147 ns	0.068 ns	0.069 ns	-0.018 ns	-0.143 ns	-0.126 ns	-0.223 ns	-0.386 ns	0.722 ***
4. PSm	0.258 *	-0.286 *	0.635 ***		-0.752 **	-0.448 ***	-0.661 ***	-0.476 ***	-0.246 ns	-0.370 **	-0.192 ns	0.446 ***	0.371 **	0.042 ns	0.167 ns	0.110 ns	-0.227 ns	-0.102 ns	0.302 *	0.209 ns	0.092 ns	0.119 ns
5.GPSa	0.372 **	0.662 ***	-0.028 ns	-0.634 ***		0.760 ***	0.837 ***	0.646 ***	0.525 ***	0.514 ***	-0.220 ns	-0.296 *	-0.287 *	-0.028 ns	-0.123 ns	-0.058 ns	0.291 *	0.070 ns	-0.296 *	-0.237 ns	-0.347 **	0.082 ns
6. GPms	0.697 ***	0.878 ***	0.263 *	-0.221 ns	0.766 ***		0.306 *	0.593 ***	0.853 ***	0.543 ***	-0.097 ns	-0.306 *	-0.213 ns	-0.181 ns	-0.281 *	-0.202 ns	0.467 ***	0.122 ns	-0.450 ***	-0.397 **	-0.464 ***	0.204 ns
7. GPts	0.237 ns	0.288 *	0.103 ns	-0.459 ***	0.749 ***	0.334 **		0.443 ***	0.103 ns	0.282 *	-0.288 *	-0.162 ns	-0.214 ns	0.118 ns	0.057 ns	0.085 ns	0.046 ns	-0.050 ns	-0.062 ns	-0.029 ns	-0.160 ns	0.022 ns
8. SIPS	0.321 *	0.569 ***	-0.013 ns	-0.359 **	0.605 ***	0.564 ***	0.317 *		0.096 ns	0.664 ***	-0.159 ns	-0.221 ns	-0.186 ns	-0.033 ns	-0.349 **	-0.320 *	0.277 *	0.191 ns	-0.198 ns	-0.252 ns	-0.331 **	-0.080 ns
9. GPSI	0.660 ***	0.717 ***	0.344 **	-0.055 ns	0.572 ***	0.862 ***	0.245 ns	0.088 ns		0.242 ns	-0.042 ns	-0.252 *	-0.111 ns	-0.168 ns	-0.105 ns	-0.028 ns	0.375 **	-0.008 ns	-0.401 **	-0.313 *	-0.353 **	0.301 *
10. SLms	0.125 ns	0.325 **	-0.092 ns	-0.178 ns	0.384 **	0.347 **	0.147 ns	0.522 ***	0.116 ns		-0.013 ns	-0.052 ns	-0.269 *	-0.134 ns	-0.320 *	-0.303 *	0.361 **	0.197 ns	-0.203 ns	-0.091 ns	-0.218 ns	0.113 ns
11.GMa	0.366 **	0.486 ***	0.102 ns	-0.231 ns	-0.026 ns	0.130 ns	-0.166 ns	0.050 ns	0.112 ns	-0.119 ns		-0.037 ns	-0.209 ns	-0.040 ns	-0.315 *	-0.278 *	0.293 *	0.224 ns	-0.475 ***	-0.503 ***	-0.204 ns	0.423 ***
12.BYm	0.647 ***	0.344 **	0.650 ***	0.386 **	0.089 ns	0.331 **	0.125 ns	0.226 ns	0.435 ***	0.055 ns	0.145 ns		0.209 ns	0.403 **	0.211 ns	0.089 ns	-0.443 ***	0.212 ns	0.207 ns	0.204 ns	0.162 ns	0.308 *
13.BYv	0.217 ns	0.031 ns	0.287 *	0.227 ns	-0.046 ns	0.080 ns	-0.042 ns	-0.010 ns	0.109 ns	-0.126 ns	-0.042 ns	0.188 ns		0.123 ns	0.504 ***	0.426 ***	-0.421 ***	-0.415 ***	0.429 ***	0.174 ns	-0.042 ns	-0.163 ns
14.PHm	0.113 ns	0.135 ns	0.048 ns	-0.041 ns	-0.029 ns	0.075 ns	-0.077 ns	0.170 ns	-0.023 ns	0.166 ns	0.143 ns	0.157 ns	0.198 ns		0.293 *	0.202 ns	-0.385 **	-0.020 ns	0.196 ns	0.112 ns	0.141 ns	0.158 ns
15.PHv	-0.182 ns	-0.156 ns	-0.140 ns	0.055 ns	-0.172 ns	-0.123 ns	-0.074 ns	-0.056 ns	-0.111 ns	-0.037 ns	-0.135 ns	-0.114 ns	0.425 ns	0.410 ***		0.963 ***	-0.491 ***	-0.560 ***	0.536 ***	0.554 ***	0.252 *	-0.112 ns
16.SER	-0.189 ns	-0.103 ns	-0.196 ns	-0..98 ns	-0.030 ns	-0.047 ns	0.011 ns	0.025 ns	-0.065 ns	-0.024 ns	-0.115 ns	-0.207 ns	0.414 ***	0.299 *	0.636 ***		-0.395 **	-0.543 ***	0.447 ***	0.502 ***	0.174 ns	-0.093 ns
17.GLN5	0.505 ***	0.550 ***	0.282 *	-0.084 ns	0.370 **	0.489 ***	0.158 ns	0.371 **	0.372 ns	0.404 **	0.315 *	0.111 ns	-0.124 ns	-0.098 ns	-0.423 ***	-0.367 **		0.143 ns	-0.642 ***	-0.547 ***	-0.363 **	0.191 ns
18.DH	-0.019 ns	0.051 ns	-0.077 ns	-0.183 ns	0.070 ns	0.064 ns	-0.011 ns	-0.085 ns	0.079 ns	-0.029 ns	0.192 ns	0.116 ns	-0.229 ns	0.086 ns	-0.434 ***	-0.452 ***	0.244 ns		-0.471 ***	-0.327 **	0.051 ns	0.060 ns
19.Chl5	-0.698 ***	-0.690 ***	-0.435 ***	0.064 ns	-0.484 ***	-0.641 ***	-0.275 *	-0.426 ***	-0.538 ***	-0.273 *	-0.332 ns	-0.238 ns	-0.007 ns	-0.011 ns	0.211 ns	0.130 ns	-0.751 ***	-0.071 ns		0.780 ***	0.402 **	-0.361 **
20.AUCPC	-0.722 ***	-0.694 ***	-0.465 ***	0.045 ns	-0.482 ***	-0.607 ***	-0.297 *	-0.452 ***	-0.483 ns	-0.347 **	-0.377 **	-0.316 *	0.035 ns	0.044 ns	0.384 **	0.311 *	-0.735 ***	-0.043 ns	0.863 ***		0.592 ***	-0.347 **
21. SSI	-0.842 ***	-0.701 ***	-0.643 ***	-0.059 ns	-0.467 ***	-0.669 ***	-0.337 **	-0.425 ***	-0.553 ***	-0.095 ns	-0.355 **	-0.365 **	-0.218 ns	-0.102 ns	0.172 ns	0.104 ns	-0.502 ***	0.043 ns	0.649 ***	0.679 ***		-0.195 ns
22. STI	0.853 ***	0.589 ***	0.738 ***	0.386 **	0.159 ns	0.515 ***	0.060 ns	0.111 ns	0.573 ***	0.115 ns	0.269 *	0.732 ***	0.140 ns	0.100 ns	-0.132 ns	-0.218 ns	0.353 ***	0.018 ns	-0.530 ***	-0.543 ***	-0.439 ***	

*See Tables 4.2, 4.5 and 4.8 for abbreviations

Table 4.12. Stepwise regression of independent characteristics on dependent grain yield of wheat genotypes grown under free drainage, transient and continuous waterlogging treatments, 1998

Independent Variable[+]	Parameter estimate	Partial R^2	Model R^2	Probability
Free drainage				
Intercept	-28.83124803			
BYm	0.09079768	0.5080	0.5080	0.0001
PHv	-0.03165117	0.0855	0.5935	0.0007
KM	0.33831304	0.0241	0.6176	0.0504
GPSa	0.39374751	0.0311	0.6487	0.0220
PS	1.69090569	0.1910	0.8397	0.0001
SIPS	-0.23426449	0.0154	0.8551	0.0094
Transient waterlogging				
Intercept	-27.23461991			
CHl	-0.00291020	0.3402	0.3402	0.0001
DH	-0.06191790	0.0656	0.5716	0.0039
KM	0.42809286	0.0383	0.6099	0.0203
BYv	-0.29964356	0.0242	0.6341	0.0570
PS	1.78952466	0.0207	0.6548	0.0721
GPSa	0.46788118	0.2364	0.8912	0.0001
GLN	-0.37761461	0.0131	0.9038	0.0084
Continuous waterlogging				
Intercept	-24.90960377			
CHl	-0.01309504	0.4870	0.4870	0.0001
BYm	0.05896009	0.2453	0.7323	0.0001
GPSa	0.5371712	0.0773	0.8096	0.0001
PS	1.13974866	0.0214	0.8310	0.0196
SIPS	0.17180129	0.0423	0.8733	0.0004
KM	0.26418810	0.0599	0.9332	0.0001

[+]See Tables 4.2, 4.2 and 4.8 for abbreviations

CONCLUSIONS

The results of this study showed that prolonged transient and continuous waterlogging stress adversely affected grain yield and growth of wheat. Continuous waterlogging, in particular, caused greater damage to the wheat plants. The results also demonstrated that large differences in the tolerance to prolonged waterlogging exist among the bread wheat genotypes studied, as indicated by significant genotype x waterlogging interactions for most of the characteristics studied. Ducula x1, PRL/Sara and HAR 604 followed by Vee/Myna were relatively tolerant to waterlogging, Et-13 and K6290-Bulk being most sensitive, and the other 10 genotypes were intermediate.

Under extreme waterlogging, percentage leaf chlorosis, biomass yield at maturity, grains per spike and kernel mass correlated highly significantly with grain yields. These characteristics also accounted for over 88% of the total variation in grain yields under continuous waterlogging stress conditions. The two yield-based indices (SSI and STI) were also correlated strongly with the different components of yield and with the most relevant characteristics of tolerance namely, number of green leaves and percentage leaf chlorosis at heading as well as area under chlorosis progress curve. Heritabilities of these characteristics and indices were large, promising a substantial gain from selection based on theme. Breeding for waterlogging stress tolerance in wheat could, therefore, be facilitated by selecting genotypes with lower percentage leaf chlorosis, higher biomass production, and greater number of grains per spike and kernel weight under the waterlogged soil conditions.

CHAPTER V

EFFECT OF SOIL WATERLOGGING ON NUTRIENT AVAILABILITY AND ITS'CONCENTRATION AND UPTAKE BY WHEAT GENOTYPES DIFFERING IN TOLERANCE

ABSTRACT

Waterlogging of soil may restrict crop performance by altering the soil mineral nutrient availability and uptake by roots. Two greenhouse experiments were conducted in 1998 and 1999 using soil with high clay content (Vertisol), at the University of the Free State, South Africa, to determine the effects of different degrees of soil waterlogging on soil nutrient availability and on the concentration and uptake of nutrients by wheat genotypes that differ in tolerance to waterlogging.

Differential responses of wheat genotypes to different waterlogging treatments were observed on vegetative dry biomass, straw and grain yields. Root zone oxygenation was significantly depressed by the waterlogging treatments as indicated by significantly reduced soil redox potentials. All 1*N* NH_4OAc (pH 7.0) soluble and exchangeable mineral nutrient concentrations in the soil increased as waterlogging severity increased. Both waterlogging and genotype treatments significantly affected the uptake and concentration of most of the nutrients in the vegetative biomass at anthesis or in the straw and grain at maturity.

A significant differential response of wheat genotypes to the waterlogging treatments was detected for several mineral nutrient concentration and uptake parameters. There was no clear cut difference among genotypes for Ca and Mg accumulation; however, compared to tolerant genotypes, sensitive genotypes appeared to accumulate more Fe, Mn, and Na nutrients although the concentrations were far below the level of toxicity reported for these nutrients, and less Cu, Zn, K, P and N with concentrations lower than the "critical" values previously reported for wheat. The results from a foliar nutrient application study

to supplement Cu, Zn and P indicated that there was a nutrient-induced improvement in waterlogging tolerance and, therefore, the adverse effects of waterlogging should be offset to some extent by foliar application of deficient nutrients.

It was concluded that there was a considerable difference between waterlogging-sensitive and tolerant wheat genotypes in their nutrient accumulation and uptake ability under waterlogging stress. The damaging effects of waterlogging were not due to Fe, Mn, or Na toxicity but were rather attributed to decreased nutrient uptake due to O_2 deficiency in the root zone, particularly P and Zn deficiencies. Selection of genotypes with greater ability to overcome the waterlogging – induced nutrient deficiencies, particularly P and Zn should improve wheat productivity on waterlogged soils. Further studies, however, are suggested to clearly define the effect of P- and Zn-nutrition on the reduced growth resulting from waterlogging and establish the mode of inheritance of tolerance to P- and Zn-deficiency associated with waterlogging stress in wheat.

Key words: Nutrient concentration; nutrient uptake, waterlogging tolerance, wheat

INTRODUCTION

Soil waterlogging adversely affects the growth of terrestrial plants (Kozlowski, 1990), primarily due to reduced oxygen (O_2) supply to the roots (Armstrong 1982). Mineral nutrition of waterlogged crop plants may be largely affected by the initial nutrient status of the soil, changes in soil physicochemical properties and the tolerance capabilities of the crop varieties (Kozlowski, 1984). In waterlogged soils, the pore spaces that usually allow free gas exchange between the rhizosphere and atmosphere are filled with water, which severely reduce the diffusion of O_2 in to the soil (Armstrong, 1982;

Ponnamperuma, 1984). Water covering the soil slows O_2 diffusion from the atmosphere by a factor of 10^{-4} (Armstrong, 1979). Respiration by roots and soil microorganisms may deplete O_2 dissolved in the soil solution within a day of waterlogging (Drew and Lynch, 1980; Ponnamperuma, 1984).

Due to the restriction of gas exchange and subsequent depletion of O_2, some soil microorganisms make use of electron acceptors other than O_2 for their respiratory oxidation (Armstrong, 1982; Ponnamperuma, 1984) thereby promoting a series of chemical and microbiological changes in the soil (Armstrong 1982). These changes result in the accumulation of CO_2 and several organic compounds to levels toxic to plant roots (Armstrong, 1982; Drew and Stolzy, 1996) and reduction of NO_3-N, Fe, Mn, and sulfate, and changes in pH and redox potential of the soil (Armstrong, 1982; Krizek, 1982; Ponnamperuma, 1984; Laanbroek, 1990). Sharma and Swarup (1989) conducted field experiments using wheat grown on alkaline soils and found a three to five fold increases in soil Fe- and Mn- concentration after six days of waterlogging. Waterlogging greatly increases Na availability particularly in sodic-alkaline soils (Sharma and Swarup, 1988, 1989; Barrett-Lennard *et al.*, 1990). Stieger and Feller (1994) found increased concentrations of NH_4-N, Mn, and Fe, decreased concentration of NO_3-N, and no change in the concentrations of Zn, Ca, K, Mg and P in a soil continuously waterlogged for 38 days. Availability of N decreases under waterlogging due to losses through volatilization and denitrification (Ponnamperuma, 1984; Belford *et al.*, 1985). Waterlogging may increase P- availability due to a release of sorbed P in the soil solution (Phillips, 1998). Due to their high solubility, Fe and Mn may become toxic for plants' growing on waterlogged soils (Krizek, 1982; Stieger and Feller, 1994). Trought and Drew (1980b) observed a decrease in the concentrations of soil NO_3-N, Ca, K, and no clear trend in P-, Mn-, and Fe -concentrations as a result of waterlogging.

The mineral composition of cultivated plants under waterlogged conditions depends largely on soil O_2 availability. It has been indicated that soil waterlogging results in reduced foliage concentrations of N, P and K in wheat (Drew and Sisworo, 1979). Stieger and Feller (1994) reported that waterlogging during grain filling reduced grain yield as well as K-, P-, Zn- and Mg- concentrations and increased Mn- and Fe-

concentrations in the shoots and grains of wheat. Leyshon and Sheard (1974) reported a reduction in N-, P- and K-concentrations of 51, 61 and 58%, respectively, in barley seedlings following short-term waterlogging. Waterlogging of barley for 10 days decreased the N-, P- and K- concentrations in grains (Stepniewski and Labuda, 1984). In a field study using wheat, Sharma and Swarup (1989) reported that short-term waterlogging decreased N-, P-, K- and Zn-uptake and led to higher uptakes of Na, Fe and Mn by the grain and straw. Huang *et al.* (1995) reported a reduction in N-, P-, K-, Mg- and Zn-concentrations in the shoots and an increase of these nutrients in the roots of winter wheat. Several of the mentioned studies have indicated that N-, P-, K- and Zn-contents in cereals were always decreased by waterlogging stress more than Mg-and Ca-contents. Waterlogging-induced O_2 deficiency may inhibit nutrient uptake and transport in waterlogging-sensitive crop varieties (Kozlowski, 1984) by altering root function due to the death of root system (Drew and Lynch, 1980; Stepniewski and Przywar, 1992; Trought and Drew, 1980a), causing nutrient leakage due to loss of integrity in root cell membranes (Resen and Carlson, 1984), or providing sub-optimal energy for active ion uptake due to inefficient anaerobic metabolism (Barrett-Lennard *et al.*, 1990; Setter and Belfod, 1990).

Waterlogging is a serious environmental constraint to wheat production on poorly drained soils (Koslowski, 1984). Vertisols with high montmorillonite clay contents are important agricultural soils in cool and wet wheat growing agroecologies of the central and eastern African highlands (Jutzi and Abebe, 1986). Wheat genotypes differ in their tolerance to waterlogging stress (Van Ginkel *et al.*, 1992). Wheat production on frequently waterlogged Vertisols such as those of the eastern African highlands could likely be improved by planting waterlogging tolerant genotypes. Little is known about the nutrient uptake and accumulation by wheat genotypes differing in waterlogging tolerance (Huang *et al.* 1995). Hence, additional research is needed to determine whether genotypic differences in waterlogging tolerance in wheat can be related to differences in nutrient acquisition and uptake. Such an understanding is important for developing tolerant genotypes and improving wheat productivity on waterlogged soils, particularly on Vertisols. This study was therefore conducted to determine the effects of different degrees of soil waterlogging on soil nutrient contents and related parameters,

and to compare the effect of waterlogging stress on the nutrient concentration and uptake by wheat genotypes identified under field and greenhouse condition to differ in waterlogging tolerance.

MATERIALS AND METHODS

Experiment One:

A soil sample from a virgin Vertisol was used in the greenhouse to fill three-liter size polyethylene pots perforated at the bottom. Sufficient soil from the top 0-20 cm depth layer was collected from Glen Agricultural College campus, located about 30 km north of Bloemfontein, South Africa. Characteristics of this soil are: 3.12% organic matter, 46% clay, 485 Ohms electrical resistance, and containing 15.2, 1.50, 57.6, 247, 35, 1158, 2240, 580 and 290 mg kg^{-1} of exchangeable Cu, Zn, Mn, Fe, P, Ca, Mg, K, and Na, respectively. The soil was pulverized and sieved to remove clogs and fibrous root materials, thoroughly mixed with nutrient solution applied at a rate of 70 mg N as KNO_3 and 35 mg P as K_2HPO_4 kg^{-1} soil. Before filling the pots with 3 kg soil, 150 g gravel was placed at the bottom to facilitate drainage of the pots.

Five bread wheat (*Tritium aestivum* L.) genotypes consisting of two waterlogging-sensitive, Et-13 and K6290-Bulk, and three waterlogging-tolerant, PRL/Sara, Vee/Myna, and Ducula, were selected based on their performance in an on-going genotype screening experiment for waterlogging tolerance. The latter three genotypes were previously identified as tolerant to waterlogging stress (Van Ginkel *et al.*, 1992) and were kindly provided by the CIMMYT/EU Eastern Africa Wheat Program. Ten seeds of each genotype were planted per pot on the 7th September 1998, covered slightly with a thin-layer of loose soil, and thinned to four seedlings after full emergence. Two pots for each genotype were used in each replication.

All the genotypes were exposed to three waterlogging treatments: 1) a control without waterlogging therefore free drainage (FD) where seedlings were grown in the pots

allowed to drain freely; 2) transient waterlogging (TWl), where seedlings grew in waterlogged pots for seven days followed by seven days free drainage in two-week cycles for a total of seven weeks; and 3) continuous waterlogging (CWl), where seedlings were subjected to permanently waterlogged conditions for seven weeks. When the seedlings reached the three to four leaf stage (i.e., 14 days old seedlings), the pots of the waterlogging treatments were each placed into a larger six-liter non-perforated polyethylene pots. Waterlogging with tap water was then initiated and the water level was maintained at 2-3 cm above the soil surface by watering daily throughout the treatment period.

The experiment was designed with four replications as a split plot with waterlogging treatments as main plots and genotypes as subplots. More replications from a nearby similar experiment were added to measure soil parameters bringing the total number of replication to eight. During the duration of the experiment, N was applied as a solution to every pot at a rate of 0.5 mg N nutrient as NH_4NO_3 at Two-week intervals to avoid leaf chlorosis, which might be induced by a N deficiency. Greenhouse temperatures were maintained at 15 ^{O}C minimum and 25 ^{O}C maximum. At flowering, all the plants from one pot from each treatment were cut at soil surface, thoroughly washed in distilled water, oven-dried at 60 ^{O}C for 72 hrs, the dry biomass was weighed and then ground to pass through a 1 mm sieve for nutrient analysis. At maturity, all the plants from the other pot were cut at 20 cm above the soil surface to avoid possibly contaminated lower plant parts, oven-dried at 60 ^{O}C for 48 hrs, the dry biomass was determined, hand-threshed and then separated into straw and grains. Both the straw and grain seeds were ground to pass through a 1 mm sieve for nutrient analysis.

Experiment Two:

This experiment was conducted in 1999 to verify the results obtained in experiment one. The purpose was to assess the effect of foliar application of selected nutrients on the survival, percentage leaf chlorosis and dry biomass production of wheat seedlings grown under continuous waterlogging stress for six weeks. Zn, Cu and P were selected as nutrients based on the results obtained in experiment one. The experiment was laid out in a randomized complete block design with three replications. The nine nutrient

treatments consisted of Zn, Cu and P sprayed separately and in combinations of two or three nutrients. A pre-planting Zn soil incorporation and a control with no application of these nutrients were also included as treatments. A separate nutrient solution was prepared for each nutrient by dissolving 0.6 g Zn as Zn $(NO_3)_2.6H_2O$, 1 g Cu as CuCl and 10.75 g P as concentrated H_3PO_4 acid in 500 ml distilled water. Solution pH was initially adjusted to 7.0 with Ca $(OH)_2$. Seventy–five milligram Zn as Zn $(NO_3)_2.6H_2O$ was applied per pot for the treatment receiving Zn as pre-planting soil incorporation. Durum wheat (*Triticum durum* L.) genotype Cocorit 71, susceptible to waterlogging stress, was planted on 20 October and was left to grow under continuous waterlogging, that was initiated on 4 November, for six weeks. Three days after waterlogging was induced, foliar nutrient application was commenced; Zn and Cu were sprayed every six days and P was sprayed every three days. Percentage leaf chlorosis was recorded four weeks after waterlogging. After six weeks, the number of seedlings that survived and the aboveground dry biomass was recorded for each treatment.

Determination of soil pH and redox potential:

Soil pH and redox potential readings were determined after three and six weeks of waterlogging. An average of four readings from replicated pots was taken for each of the three waterlogging treatments using an appropriate platinum electrode. Measurements were made by inserting the electrode directly into the soil to a depth of 10 cm below the soil surface.

Soil analyses:

The soluble and exchangeable soil mineral nutrient contents were determined for each treatment. After six weeks of waterlogging, two sets of soil samples were collected from randomly selected replicate pots in each of the three waterlogging treatments. The samples were taken at a depth of 10 cm below the soil surface. The first set of the soil samples was immediately placed on filter paper in a funnel, leached through with 1*N* NH_4OAc (pH 7.0) to collect 100 ml leachate from each sample. After proper dilution, Fe and Mg (presumed to be reduced), K, Na, Ca and Mg were determined using Atomic Absorption Spectrometry. The second set of the soil sample was air dried at room temperature, ground to pass through a 2 mm sieve. Sub-samples of 2.5 g were shaken

for 30 min. in 1*N* $NaHCO_3$ (pH 8.5) and filtered. P was then determined in the leachates using the sulfuric acid-ammonium molybdate colorometric method (Hesse, 1971).

Plant analyses:

Plant mineral nutrient concentrations were determined for the whole-plant biomass at anthesis and straw and grain at maturity for each genotype. Sub-samples of 2g were dry-ashed at 550 ^{o}C, digested in nitric acid on a hot sand-bath, dissolved in diluted HNO_3, filtered into a volumetric flask and made to volume. The concentrations of Cu, Zn, Mn, Fe, Na, K, Mg and Ca were determined after proper dilution by Atomic Absorption Spectrometry. P was determined colorometrically using the ammonium vanadate-molybdate method (Hesse, 1971). N was determined by Kjeldahl digestion and distillation procedure using 0.1 g sub-samples digested overnight in sulfuric acid in the presence of hydrogen peroxide. Nutrient-uptake was calculated by multiplying each nutrient concentration value with its respective biomass, straw or grain masses.

Statistical analyses:

All the measured soil, nutrient and plant parameters were subjected to appropriate analysis of variance using MSTAT-C micro-software. The data on soil parameters and the plant response in the foliar application trial were analyzed as a randomized complete block design while all other data were analyzed as split plot design. Differences among significant treatment means were separated using least significant differences (LSD) at $P \leq 0.05$.

RESULTS AND DISCUSSION

Soil redox potential (Eh) and pH:

The effects of waterlogging on the soil Eh and pH readings after three and six weeks of waterlogging are shown in Table 5.1. Soil Eh was greatly lowered by waterlogging. For

both readings, continuous waterlogging gave significantly lower Eh-values than transient waterlogging, which in turn, gave significantly lower values than freely drained soils. The drop in Eh was much higher after six weeks compared to three weeks. It is generally accepted that an adequate O_2 supply to the root zone environment is essential for optimum plant growth and nutrient uptake. Oxygen is generally considered deficit around 350 mV at pH 7 on the Eh-scale (Armstrong, 1979, 1982; Krizek, 1982; Ponnamperuma, 1984; Laanbroek, 1990). In our study, the Eh-values of the waterlogged soils, especially in CWl soils, remained much lower than 350 mV (Table 5.1), suggesting that root zone oxygenation was significantly depressed by waterlogging which is in agreement with results reported by Davies and Hillman (1988), Musgrave (1994) and Thomson *et al.* (1992). Waterlogging reduced soil pH-values at both readings in a similar manner as for Eh. Compared to the FD-treatment, pH-values were reduced respectively by 0.23 and 0.59 units under TWl- and CWl- treatments after three weeks and by 0.23 and 0.49 units after six weeks. Increased concentrations of CO_2, an anaerobic metabolic products and reduced mineral nutrients (Laanbroek, 1990) probably contributed towards reducing pH-values under waterlogging.

Table 5.1. Mean effects of waterlogging on soil pH and redox potential, 1998/99

Waterlogging	Redox potential (mV)		Soil pH	
	3-wk[+]	6-wk	3-wk	6-wk
Free drainage	394a	410a	7.15a	7.20a
Transient	271b	163b	6.92b	6.92b
Continuous	135c	10c	6.61c	6.71b
P	***	***	***	***
LSD (0.05)	21	37	0.11	0.25
Mean	266.67	194.33	6.89	6.94
C.V. (%)	7.58	17.73	1.45	3.27

, * Represent significance level at 0.01 and 0.001 probability, respectively. [+]wk = week; Means followed by the same latter are not significantly different at 0.05 probability level.

Soil nutrient concentrations:

The effect of waterlogging on the nutrient concentrations in the soils at the termination of the experiment are shown in Table 5.2. The concentration of Fe and Mn in the soil greatly increased as a result of waterlogging, especially in the CWl-treatment. Fe- and MN-concentrations were intermediate in the TWl-treatment and negligible in the FD soils. The rise in Fe- and Mn-concentrations under waterlogged conditions can be attributed to the reducing conditions created within the soil system as was indicated by lower Eh measurements (Table 5.1), which is in agreement with the findings of Davies and Hillman (1988), Musgrave *et al.* (1994) and Stieger and Feller (1994). In waterlogged soils, Fe^{+++} and Mn^{+++} are concentrated as reduced and more soluble Fe^{++} and Mn^{++} forms (Ponnamperuma, 1984), which are more readily absorbed by roots. As reported by Bjerre and Schierup (1985) and Iu *et al.* (1981), waterlogging also resulted in the release of Mn and Fe from the organic and oxide bound reservoirs into the soluble, exchangeable and inorganic reservoirs.

The concentration of P in the soil was increased by the waterlogging treatments. The higher P- concentration in waterlogged soils may suggest a release of sorbed P from soil materials under waterlogging. Phillips (1998) reported that the 1*M* NaOAc (pH3.0) extractable P-concentration in the soil increased over a period of waterlogging, and attributed it to solubilization of Fe $(OH)_3$ materials under reducing conditions with an accompanying release of sorbed and occluded P. The concentration of soil-K increased significantly with waterlogging. Compared to the concentration in the FD-treatment, the concentrations of K in the soils increased by 74.7 % under TWl-treatment and by 120.7% under CWl-treatment. Soil waterlogging also increased the concentrations of Ca and Na in the soil, but the differences were not statistically significant. The Mg-concentrations of the soils were not affected by the waterlogging treatments.

Table 5.2. Mean effects of waterlogging on mineral nutrient concentration in the soil, 1998/99

	Soil mineral nutrient (mg/kg dry soil)						
Waterlogging	Fe	Mn	P	K	Ca	Mg	Na
Free drainage	0.37b[+]	1.83c	24.1b	173.60c	1062.28b	1151	171.34b
Transient	1.71b	44.93b	28.0ab	303.26b	1608.24a	2322	411.59a
Continuous	6.30a	114.81a	35.4a	383.20a	1805.70a	2212	454.68a
P	***	***	**	**	*	Ns	***
LSD (0.05)	1.53	33.00	4.93	66.79	238.60	------	71.89
Mean	2.79	53.86	27.17	286.71	1492.07	1895.00	345.87
C.V. (%)	51.16	57.14	16.92	32.17	22.08	55.81	28.70

*, **, *** Represent significance level at 0.05, 0.01 and 0.001 probabilities, respectively. Ns represent non-significance. Means followed by the same latter are not significantly different at 0.05 probability level.

Grain yield and biomass:

Soil waterlogging markedly reduced the growth of all the wheat genotypes (Table 5.3). Under waterlogged soil conditions, plants were visually stressed, stunted and showed yellowing of foliage typical of N deficiency. In some genotypes, yellowing of leaf veins followed by browning was common in waterlogged treatments. Sensitive genotypes, particularly K6290-bulk showed leaf purpling. This probably indicated the presence of other abnormalities in growth. Shortening of internodes and leaves was serious on waterlogged Et-13. Wheat genotypes obviously differed in their response to the waterlogging treatments and there was a significant waterlogging x genotype interaction for all plant parameters considered (Table 5.3). Increased waterlogging severity caused a greater reduction of vegetative dry biomass, straw and grain yields for the sensitive Et-13, K6290-bulk genotypes and also for the tolerant genotype Vee/Myna and Ducula. Of the susceptible genotypes, Et-13 appeared to be more sensitive to continuous waterlogging and K6290-bulk to transient treatment. Vee/Myna and Ducula were the

most tolerant genotypes to waterlogging as shown by their better yielding ability than the other three genotypes. In a field study in Mexico, Ginkel *et al.* (1992) have previously identified these genotypes as tolerant to extended waterlogging stress. Davies and Hillman (1988) also reported differential biomass and yield response of tetraploid and hexaploid wheat populations to waterlogging.

Table 5.3. Mean effects of waterlogging x genotype interaction on whole plant dry biomass at anthesis, and final straw and grain yield of wheat, 1998/99

Genotype	Dry biomass at anthesis			Straw yield			Grain yield		
	FD	TWl	CWl	FD	TWl	CWl	FD	TWl	CWl
	g/plot								
Et-13	37.22	33.32	16.06	35.24	28.62	19.76	30.08	25.60	13.05
K 6290-bulk	37.13	29.88	24.41	30.51	24.55	22.82	26.85	17.69	15.00.
Vee/Myna	34.38	27.74	27.08	28.61	23.96	23.45	26.46	22.95	19.67
PRL/Sara	32.14	21.24	15.70	31.97	24.46	21.45	23.50	20.85	14.38
Ducula	29.67	28.47	19.15	27.71	23.00.	21.99	23.59	21.86	19.37
LSD (0.05)		4.50			3.11			2.908	

FD-Freely drained control; TWl-transient waterlogging; CWl-continuous waterlogging.

Iron and manganese concentrations and uptake:

The effect of waterlogging on whole plant, straw and grain Fe- and Mn- concentrations and whole plant and straw uptake of these nutrients differed among genotypes as indicated by a significant waterlogging x genotype interaction (Tables 5.6 and 5.7). Increasing severity of waterlogging resulted in significantly higher Fe- and Mn-concentrations in the sensitive Et-13 and K6290-bulk genotypes than in the tolerant Vee/Myna, PRL/Sara or Ducula. Et-13 showed the highest Fe- and Mn- concentrations in the CWl-treatment whereas K6290-bulk showed the highest concentration of these nutrients in the TWl-treatment. Unlike concentration, the whole plant Fe- and Mn-

uptake decreased for the tolerant genotypes with no significant differences for Et-13 and K6290-bulk. There was no interaction effect observed on grain Fe- and Mn- uptake. Huang *et al.*, (1995) found higher shoot Fe- and Mn-concentrations in the sensitive "Bayles" wheat genotype compared to a tolerant "Savanah". Soil waterlogging and genotype main effects were also significant for most Fe- and Mn- concentrations (Table 5.4) and uptake parameters (Table 5.5). The sensitive genotypes, Et-13 and K6290-bulk had higher concentrations and uptake of Fe and Mn than the relatively tolerant genotypes except for grain Mn-uptake. Waterlogging, especially the CWl-treatment increased the whole plant, straw and grain Fe- and Mn- uptake and concentrations. Uptake values were intermediate for the TWl- and lowest for the FD-treatment. Increases in straw and grain Fe- and Mn- concentrations and uptake were reported in waterlogged wheat (Sharma and Swarup, 1989; Stieger and Feller, 1994) and oats (Bjerre and Schierup, 1985). Increases in Fe and Mn concentrations could lead to toxicity. The average concentrations of Fe and Mn measured at anthesis indicated that the Fe-concentrations fell within the "optimum" nutrient range reported by Bergmann (1992), Mn-concentrations of the freely drained plants fell below the "critical" value reported by Melsted *et al.*, (1969) and the values for the waterlogged plants were comparable to the critical values (Table 5.9). The observed increases in Fe- and Mn-concentrations in the vegetative biomass at anthesis (Tables 5.4 and 5.5) and in the soil (Table 5.2), due to waterlogging, were therefore lower than the Fe- and Mn-concentrations required to induce toxicity in cereals as cited by Bergmann (1992) and Sharma and Swarup (1989). Toxic concentrations of Fe and Mn generated through reducing conditions were, therefore, not implicated in our experiment, which is in agreement with findings of Leyshon and Sheard (1974), Trought and Drew (1980b) and Sharma and Swarup (1989).

Table 5.4. Mean mineral concentration and statistical significance of treatment effects in bread wheat genotypes, 1998/99

Mineral nutrient concentration

Factor	Cu	Zn	Fe	Mn	Ca	Mg	K	Na	P	N
	mg/kg D.M.				*mg/g D.M.*				*(%)*	
	Whole plant									
Waterlogging (Wl)	**NS**	***	**	**	*	**Ns**	***	***	***	***
Free drainage	5.5	14.8a	149.8b	20.6c	1.20b	1.76	21.15a	0.17c	0.162a	2.08a
Transient	5.5	8.0b	142.6b	29.0b	1.19b	1.67	15.09b	1.00a	0.132b	1.67b
Continuous	4.6	6.8b	187.1a	40.1a	1.39a	1.78	12.75c	0.92b	0.106c	1.13c
LSD (0.05)	---	1.75	22.60	7.53	0.17	--	1.40	0.07	0.016	0.17
Genotype (G)	**NS**	***	**	***	***	***	**Ns**	**	**	**Ns**
Et-13	5.3	9.0b	185.5a	35.7a	1.17cd	1.62b	16.96	0.52c	0.126bc	1.62
K6290-Bulk	5.2	9.5b	174.0ab	31.6a	1.39a	1.77a	15.20	0.76a	0.110c	1.54
Vee/Myna	5.2	8.5b	144.8c	25.9d	1.10d	1.58b	15.95	0.75ab	0.136ab	1.58
RL/Sara	5.2	11.2a	156.9c	28.3bc	1.36ab	1.87a	16.64	0.68bc	0.146ab	1.72
Ducula	5.3	11.1a	140.0c	27.3cd	1.26bc	1.85a	16.91	0.64c	0.152a	1.66
LSD (0.05)	---	1.55	26.34	2.85	0.11	0.14	------	0.07	0.020	------
Wl x G	**NS**	**NS**	***	***	**	*	**Ns**	**Ns**	**Ns**	**Ns**
C.V. (%)	17.66	19.06	19.91	11.51	10.63	9.52	13.97	12.41	17.55	13.82
	Straw									
Waterlogging (Wl)	**Ns**	*	***	***	***	***	***	***	*	**Ns**
Free drainage	2.15	6.28a	159.8c	15.3c	1.19c	1.67b	19.25a	0.70c	0.028b	0.67
Transient	2.75	4.22b	219.9b	25.7b	1.90a	2.27a	18.79a	18.80a	0.034b	0.71
Continuous	1.95	4.22b	280.5a	32.0a	1.76	2.36a	13.70b	11.37b	0.052a	0.58
LSD (0.05)	-----	1.57	32.55	4.23	0.13	0.24	1.57	0.26	0.014	----
Genotype (G)	**Ns**	*	***	*	*	***	***	***	**	**Ns**
Et-13	2.13	4.71b	287.5a	25.1ab	1.40b	1.74c	15.52c	0.76c	0.038b	0.57
K6290-Bulk	2.50	4.83b	257.5a	26.3a	1.71a	2.04b	16.75bc	12.62b	0.032b	0.66
Vee/Myna	2.42	4.58b	168.8b	23.3bc	1.58ab	2.04b	19.36a	16.24a	0.034b	0.69
PRL/Sara	2.13	4.50b	192.8b	21.8c	1.73a	2.30a	16.68bc	12.48	0.036b	0.66
Ducula	2.21	5.92a	193.8b	25.3a	1.65a	2.36a	17.91ab	13.01	0.048a	0.70
LSD (0.05)	-----	1.00	33.58	2.41	0.23	0.24	1.71	0.19	0.008	-----
Wl x G	**Ns**	**Ns**	***	***	*	*	**	**Ns**	**Ns**	**
C.V. (%)	22.73	24.63	18.43	15.44	17.23	13.59	11.97	18.65	25.95	18.68
	Grain									
Waterlogging (Wl)	**	*	***	***	**	*	*	***	**	**Ns**
Free drainage	6.52a	21.5a	88.6c	25.3c	0.19c	1.10	2.65a	0.048c	0.372a	2.52
Transient	6.40a	20.6a	105.1b	29.8a	0.25a	1.12	2.46ab	0.063a	0.316b	2.79
Continuous	3.97b	16.8b	157.3a	34.6a	0.22b	1.19	2.32b	0.055b	0.284b	2.72
LSD (0.05)	1.32	3.34	13.43	2.78	0.023	0.05	0.24	0.045	0.040	----
Genotype (G)	**	***	*	**Ns**	***	***	***	**	***	***
Et-13	4.46b	15.5c	127.0a	29.6	0.18b	1.03c	2.15c	0.064a	0.292b	2.34c
K6290-Bulk	6.17a	19.1b	124.8ab	30.4	0.23a	1.16b	2.64a	0.062a	0.360a	2.58b
Vee/Myna	5.46a	17.8bc	105.2c	29.0	0.21a	1.11b	2.46b	0.049bc	0.288b	2.61b
PRL/Sara	5.96a	22.5a	117.9abc	30.3	0.23a	1.15b	2.32b	0.045c	0.328a	2.97a
Ducula	6.13a	22.6a	110.0bc	30.1.	0.23a	1.24a	2.80a	0.057ab	0.358a	2.90a
LSD (0.05)	0.88	2.38	15.94	-----	0.025	0.06	0.17	0.012	0.036	0.19
Wl x G	*	*	***	***	**Ns**	*	**Ns**	***	***	***
C.V. (%)	18.78	14.75	16.45	12.44	13.85	6.35	8.06	26.17	13.00	8.65

*, **, *** Represent significance at 0.05, 0.01 and 0.001 probability levels, respectively. Ns represent non-significance. Means followed by the same letter are not significantly different at 0.05 probability level.

Table 5.5. Mean mineral nutrient uptake and statistical significance of treatment effects in bread wheat genotypes, 1998/99

Mineral nutrient uptake (mg/pot)

Factor	Cu	Zn	Fe	Mn	Ca	Mg	K	Na	P	N
	Whole plant									
Waterlogging (Wl)	**	***	**	Ns	**	***	***	***	***	***
Control	0.19a	0.50a	5.06a	0.69	40.85a	59.94a	716.76a	5.82c	55.2a	707.0a
Transient	0.15a	0.22b	4.05b	0.82	32.89b	46.26b	418.47b	28.09a	37.0b	458.0b
Continuous	0.09b	0.13c	3.81b	0.81	27.93b	35.90c	256.00c	19.08b	21.1c	227.0c
LSD (0.05)	0.047	0.033	0.60	----	5.97	6.55	5.19	2.38	7.4	73.8
Genotype (G)	*	Ns	***	***	***	***	***	***	Ns	***
Et-13	0.16a	0.28	4.75ab	0.89a	31.92b	45.12b	507.46a	16.86b	38.8	498.0a
K6290-Bulk	0.16a	0.31	5.22a	0.90a	42.50a	54.75a	476.82c	21.17a	35.4	487.8a
Vee/Myna	0.16a	0.26	4.35bc	0.76b	32.54b	47.08b	484.55b	21.07a	40.6	478.9a
PRL/Sara	0.12b	0.28	3.60c	0.64c	30.54b	42.72b	404.59e	13.56c	34.2	417.2b
Ducula	0.14ab	0.30	3.62c	0.68bc	31.95b	47.17b	445.30d	15.65bc	39.8	438.2b
LSD (0.05)	0.025	----	0.81	0.11	3.83	4.66	4.36	2.95	-----	40.5
Wl x G	Ns	Ns	*	**	***	***	*	***	**	**
C.V. (%)	21.21	18.87	22.71	17.62	13.65	11.89	11.35	20.14	17.01	10.55
	Straw									
Waterlogging (Wl)	Ns	***	Ns	*	**	Ns	***	***	Ns	*
Control	0.07	0.19a	4.94	0.50b	36.40b	50.99	589.20a	21.02b	8.4	209.6a
Transient	0.07	0.10b	5.53	0.64a	46.90a	56.10	464.06b	46.16	8.2	174.0ab
Continuous	0.04	0.09b	6.04	0.70a	38.40a	51.79	301.26c	25.58b	11.4	127.0b
LSD (0.05)	-----	0.033	----	0.15	4.80	------	6.22	6.63	---	62.7
Genotype (G)	Ns	Ns	***	Ns	Ns	*	Ns	***	**	Ns
Et-13	0.06	0.13	7.29a	0.64	38.32	46.98b	451.66	20.41c	9.8ab	164.1
K6290-Bulk	0.07	0.13	6.43a	0.65	43.55	52.66ab	442.51	31.62b	8.2b	176.4
Vee/Myna	0.06	0.12	4.25b	0.57	39.72	51.00ab	494.79	40.11a	8.4b	173.3
PRL/Sara	0.06	0.12	4.9b	0.55	42.27	56.94a	433.08	31.33b	8.6b	168.2
Ducula	0.05	0.15	4.62b	0.68	38.97	57.17a	435.48	30.64b	11.4a	169.2
LSD (0.05)	-----	----	0.90	-----	-------	6.73	--------	4.70	2.0	------
Wl x G	Ns	Ns	**	**	*	Ns	**	*	Ns	**
C.V. (%)	25.16	28.52	19.67	15.32	18.12	15.35	12.46	18.41	24.83	20.83
	Grain									
Waterlogging (Wl)	**	***	Ns	**	***	***	***	***	***	**
Control	0.16a	0.54a	2.27	4.02a	4.93a	28.11a	67.78a	1.20b	9.83a	644.8a
Transient	0.13b	0.40b	2.27	3.13b	5.43a	24.53b	54.20b	1.41a	6.73a	614.6a
Continuous	0.07c	0.29c	2.50	2.96b	3.53b	19.41c	38.02c	0.59c	4.98b	446.0b
LSD (0.05)	0.04	0.06	-----	0.41	0.63	1.90	2.68	0.06	1.8	71.7
Genotype (G)	Ns	***	Ns	***	Ns	***	***	***	Ns	***
Et-13	0.10	0.35c	2.47	3.04c	4.23	23.02b	49.92cd	1.46a	6.99	535.5cd
K6290-Bulk	0.12	0.39bc	2.33	3.49ab	4.57	22.83b	53.18bc	1.17b	7.18	518.4d
Vee/Myna	0.12	0.41b	2.38	3.35bc	4.86	25.42a	56.95ab	1.11bc	6.85	596.4ab
PRL/Sara	0.12	0.42b	2.22	3.14bc	4.44	22.15b	45.60d	0.86c	7.11	567.0bc
Ducula	0.13	0.49a	2.33	3.85a	5.04	26.67a	61.02a	1.23ab	7.71	625.0a
LSD (0.05)	-----	0.05	-----	0.37	-----	2.07	5.13	0.25	-----	43.5
Wl x G	*	***	Ns	Ns	***	***	***	***	**	***
C.V. (%)	23.71	13.48	17.03	13.39	18.37	10.39	11.62	25.63	12.87	9.34

*,**,*** represent significance at 0.05, 0.01, 0.001 probability levels, respectively. Ns represent non-significance. Means followed by the same letter are not significantly different at 0.05 probability level.

Copper and zinc concentrations and uptake:

A significant waterlogging x genotype interaction was detected for the Zn- and Cu-concentrations in and -uptake by grains (Tables 5.5 and 5.6). Grain Zn- concentration and uptake, and Cu-ˆ uptake reduced significantly for all genotypes as waterlogging severity increased, to a greater extent for the sensitive Et-13 and K6290-bulk. Cu-concentration slightly increased, although not significantly, for all genotypes with the exception of Et-13 in the TWl- treatment. Huang *et al.* (1995) also reported a greater reduction in shoot Zn- concentration for sensitive genotypes than for tolerant genotypes when waterlogged. Waterlogging caused a significant decrease in all the Zn-concentration and -uptake parameters (Tables 5.4 and 5.5). Concentration and uptake values were highest for the FD-, intermediate for the TWl- and lowest for the CWl-treatments for all the parameters. Decreasing Zn-concentrations due to waterlogging was reported in wheat (Sharma and Swarup, 1989) and sorghum (Maranville *et al.*, 1986). Cu-concentration in the grain and -uptake by both the whole plant and grain were significantly decreased by waterlogging (Tables 5.4 and 5.5). Maranville *et al.* (1986) also reported a reduction in Cu- concentration in sorghum at booting stage by more than 50% in response to waterlogging for several genotypes studied. Bjerre and Schierup (1985) reported significantly reduced plant Cu- and Zn-uptakes in waterlogged oats. A significant difference among genotypes was detected in grain Cu-concentration and its uptake by the whole plant. The Zn-concentration in the whole plant, straw and grains and its uptake by grain differed significantly among genotypes (Tables 5.4 and 5.5). Tolerant genotypes had significantly higher concentrations and uptake of Zn. Significant variations among genotypes in Cu- and Zn-concentrations were reported in waterlogged sorghum (Maranville *et al.*, 1986). In comparison with the nutrient sufficiency values previously published for wheat (Bergmann, 1992, Melsted *et al.*, 1969), the average concentrations of both Zn and Cu in waterlogged plants dropped below the "critical" level of 0.50 and 1.50 %, respectively, indicating that Zn and Cu nutrient deficiencies occurred in waterlogged plants. This was confirmed by the results from the foliar nutrient application trial, which involved the application of Cu, Zn and P (Table 5.8). Foliar application of Cu and Zn increased the number of seedlings with green leaves significantly, reduced the percent of leaf chlorosis and gave the highest dry

biomass yield for continuously waterlogged wheat after six weeks. The plants were also greener and more vigorous when sprayed with Cu, Zn or both nutrients than any of the other treatments (Figure 5.1). Uptake and metabolism of Zn is disturbed by high concentrations of P in the soil, especially when accompanied by high pH values and high clay and organic matter contents of the soil (Bergmann, 1992). The experimental soil had high organic matter (3.12%) and clay (46%) content, and the pH-values (Table 5.1) during experimental period remained well within the range (6.5-8.0) reported to cause Zn-deficiency (Bergmann, 1992). Therefore, the low Zn-concentrations and uptake observed under waterlogging in this experiment (Tables 5.4 and 5.5) could partly be attributed to an increased P-concentration which exacerbates soil Zn- deficiency by enhancing bonding of Zn to oxides and hydroxides of Fe (Loneragan *et al.*, 1979) and to free organic oxides and bicarbonates (Forno *et al.*, 1975) in waterlogged soils.

Table 5.6. Mean effects of waterlogging x genotype interaction on the mineral nutrient concentration of bread wheat, 1998-99

A. Whole plant

Genotype	Fe			Mn			Ca			Mg		
	FD	TWI	CWI	FD	TWI	CWI	FD	TWI	CWI	FD	TWI	CWI
	mg/kg D.M.						mg/g D.M.					
Et-13	126	155	269	22	30	56	1.03	1.04	1.45	1.50	1.53	1.82
K6290-bulk	143	161	218	17	33	46	1.54	1.24	1.38	2.00	1.68	1.64
Vee/Myna	161	124	150	19	27	32	1.01	1.08	1.21	1.61	1.52	1.62
PRL/Sara	166	136	165	23	30	34	1.22	1.37	1.49	1.84	1.88	1.91
Ducula	153	134	134	23	25	34	1.17	1.21	1.41	1.87	1.76	1.93
LSD 0.05)		45.63			4.93			0.19			0.24	

B. Straw

Genotype	Fe			Mn			K			Ca			Mg			N		
	FD	TWI	CWI	FD	TWI	CWI	FD	TWI	CWI	FD	TWI	CWI	FD	TWI	CWI	FD	TWI	CWI
	mg/kg D.M.						mg/g D.M.									%		
Et-13	161	263	438	14.3	22.9	38.3	18.40	16.71	11.45	1.13	1.57	1.50	1.36	1.88	1.98	0.69	0.54	0.47
K6290-bulk	149	277	346	11.5	33.0	34.5	21.39	16.46	12.39	1.45	1.93	1.74	1.88	2.25	2.00	0.85	0.69	0.43
Vee/Myna	149	267	190	16.4	22.1	31.3	21.79	20.51	15.79	1.33	1.74	1.67	1.65	2.08	2.40	0.63	0.81	0.62
PRL/Sara	171	200	208	15.8	23.0	26.8	16.00	19.44	14.60	0.91	2.15	2.13	1.53	2.53	2.84	0.57	0.69	0.73
Ducula	168	192	221	18.4	27.4	29.8	18.66	20.80	14.26	1.11	2.09	1.73	1.94	2.61	2.60	0.63	0.80	0.66
LSD 0.05)		58.2			5.39			2.96			0.19			0.41			0.18	

C. Grains

Genotype	Fe			Mn			Cu			Zn			Mg			Na			P			N		
	FD	TWI	CWI	FD	TWI	CWI	FD	TWI	CWI	FD	TWI	CWI	FD	TWI	CWL	FD	TWI	CWI	FD	TWI	CWI	FD	TWI	CWI
	mg/kg DM												mg/g DM						%					
Et-13	81	83	217	21	23	45	5.3	4.5	3.6	17	17	13	0.97	0.96	1.16	39	101	51	0.42	0.24	0.22	2.36	2.35	2.30
K6290-bulk	86	136	153	24	34	33	6.4	7.0	5.1	23	17	17	1.12	1.17	1.19	44	73	69	0.40	0.34	0.34	2.74	2.68	2.31
Vee/Myna	91	100	124	26	32	29	5.5	6.5	4.4	20	18	15	1.11	1.12	1.10	44	47	55	0.28	0.28	0.28	2.40	2.74	2.68
PRL/Sara	93	107	153	27	30	34	7.0	7.5	3.4	21	18	19	1.06	1.12	1.26	42	43	48	0.40	0.24	0.34	2.49	3.18	3.25
Ducula	92	99	139	29	30	32	7.0	8.0	3.4	24	23	20	1.23	1.22	1.26	68	51	52	0.32	0.32	0.32	2.61	3.02	3.08
LSD 0.05)		27.6			5.3			1.5			4.1			0.10			20.7			0.06			0.33	

Table 5.7. Mean effects of waterlogging x genotype interaction on the mineral nutrient uptake of bread wheat, 1998

A. Mineral nutrient uptake by whole plant at anthesis (mg/pot)

Genotype	Fe			Mn			P			Na			N			K			Mg			Ca		
	FD	TWI	CWI	FD	TWI	CWI	FD	TWI	CWI	FD	TWI	CWI	FD	TWI	CWI	FD	TWI	CWI	FD	TWI	CWI	FD	TWI	CWI
Et-13	4.70	5.18	4.39	0.80	1.00	0.88	60.4	41.6	14.4	5.71	30.76	14.12	780.3	530.9	182.7	797	486	240	57	51	29	38	35	23
K6290-Bulk	5.28	4.89	5.51	0.62	1.00.	1.11	56.6	31.6	18.0	5.96	33.32	24.25	748.4	460.3	254.6	727	420	283	74	50	40	57	37	34
Vee/Myna	5.57	3.45	4.02	0.65	0.77	0.87	53.4	40.0	28.2	6.79	28.50	27.93	691.4	456.6	288.6	714	423	316	55	42	44	35	30	33
PRL/Sara	5.29	2.95	2.55	0.73	0.65	0.54	54.6	27.2	20.4	5.04	21.94	13.70	691.5	379.9	180.2	702	326	189	59	39	30	39	29	24
Ducula	4.48	3.80	2.56	0.68	0.73	0.64	50.4	44.4	24.8	5.60	25.96	15.40	623.7	462.4	228.6	647	441	251	56	49	36	35	34	27
LSD (0.05)		1.40			0.20			4.6			5.10			70.2			7.55			8.08			6.63	

B. Mineral nutrient uptake by straw at maturity (mg/pot)

Genotype	Fe			Mn			Ca			K			Na			N		
	FD	TWI	CWI	FD	TWI	CWI	FD	TWI	CWI	FD	TWI	CWI	FD	TWI	CWI	FD	TWI	CWI
Et-13	5.7	7.6	8.6	0.50	0.66	0.76	39.9	45.0	30.0	648	479	228	8.5	40.1	12.6	241.9	156.2	94.2
K6290-Bulk	4.6	6.8	7.9	0.35	0.81	0.78	43.8	47.4	39.9	643	404	280	20.2	48.4	26.3	261.9	169.4	97.7
Vee/Myna	4.3	4.0	4.5	0.47	0.53	0.73	38.2	41.7	39.1	625	491	369	29.2	50.2	41.0	182.0	194.8	143.1
PRL/Sara	5.5	4.8	4.5	0.51	0.56	0.57	29.3	52.0	45.5	513	472	315	24.4	44.4	23.3	182.5	168.5	153.5
Ducula	4.7	4.4	4.8	0.51	0.63	0.65	30.8	48.2	37.9	517	475	314	20.9	47.8	23.4	179.5	181.2	146.8
LSD (0.05)		1.6			0.14			10.5			8.07			8.2			50.8	

C. Nutrient uptake by grain at maturity (mg/pot)

Genotype	Cu			Zn			Ca			Mg			K			Na			P			N		
	FD	TWI	CWI	FD	TWL	CWI	FD	TWI	TWI	FD	TWI	CWI	FD	TWI	CWI	FD	TWI	CWI	FD	TWI	CWI	FD	TWI	CWI
Et-13	0.16	0.11	0.05	0.52	0.44	0.17	5.0	5.5	2.2	29	25	15	71	52	27	1.2	2.6	0.7	12.0	6.1	2.8	709.0	599.0	298.4
K6290-Bulk	0.17	0.12	0.08	0.61	0.30	0.26	5.8	4.5	3.3	30	21	18	76	47	36	1.2	1.3	1.0	10.5	6.0	5.1	736.0	474.6	344.5
Vee/Myna	0.14	0.13	0.09	0.52	0.41	0.30	4.7	5.7	4.3	29	25	22	69	58	45	1.2	1.1	1.1	8.3	6.5	5.8	636.4	626.4	526.5
PRL/Sara	0.16	0.15	0.06	0.49	0.39	0.28	4.7	5.2	3.4	25	23	18	57	45	34	1.0	0.9	0.7	9.4	7.1	4.9	577.4	659.4	464.2
Ducula	0.16	0.16	0.07	0.58	0.48	0.43	4.5	6.2	4.4	27	29	24	67	69	49	1.5	1.2	1.0	8.9	8.0	6.3	565.2	713.3	596.5
LSD (0.05)		0.04			0.08			1.2			3.6			8.9			0.4			1.06			75.0	

Figure 5.1. Pictures depicting the response of continuously waterlogged wheat to foliar applications of Zn, Cu, and P nutrients.

Nitrogen and phosphorus concentrations and uptake:

There were significant interactions between waterlogging and genotypes for all the N-concentration and uptake parameters except for the whole plant N-concentration (Tables 5.6 and 5.7). Waterlogging significantly reduced the straw N-concentration for the

sensitive Et-13 and K6290-bulk while it increased slightly for all other genotypes. Increased severity of waterlogging significantly reduced the grain N-concentration for K6290-bulk and it increased for the tolerant Vee/Myna, PRL/Sara and Ducula. N-uptake by all the plant components were significantly reduced for all genotypes by waterlogging, but the degree of reduction was the highest for the sensitive Et-13 and K6290-bulk genotypes. The effect of waterlogging on grain P-concentration and whole plant and grain P-uptake also depended on wheat genotypes (Table 5.6 and 5.7). Grain P-concentration significantly increased in Et-13, K6290-bulk and PRL/Sara in response to waterlogging, especially for the CWl-treatment, and decreased in Vee/Myna and Ducula, especially in the TWl-treatment. Whole plant grain P-uptake significantly decreased for all genotypes as severity in waterlogging increased. The reduction was, however, greater for Et-13 and K6290-bulk than for the other genotypes. Huang *et al.* (1995) reported significant differences in shoot and root N- and P-concentrations between sensitive and tolerant wheat genotypes waterlogged. Whole plant, straw and grain P-concentrations as well as straw and grain P-uptake were significantly different among the wheat genotypes studied (Tables 5.4 and 5.5). P-uptake by and -concentration in the whole plant, straw or grain were greater for one or more of the tolerant genotypes than for the more sensitive Et-13 and K6290-bulk. N-uptake by and -concentration in the grain were greater in the tolerant PRL/Sara and Ducula, and lower for the sensitive Et-13 and K6290-bulk genotypes. The whole plant N-uptake was significantly higher for Et-13, K6290-bulk and Vee/Myna due to their greater biomass production (Table 5.3). Straw and grain N-concentration and straw N-uptake was hardly influenced by waterlogging. Concentration and uptake parameters for both P and N slightly decreased with increased waterlogging stress except for the straw and grain P-concentrations that were higher for CWl compared to the other treatments (Tables 5.4 and 5.5). When compared with "critical" and "sufficiency" nutrient levels (Table 5.9), both the P- and N- concentrations were well below the "critical" value reported by Melsted *et al.* (1969), indicating that the waterlogged plants were deficient in these nutrients. The reduction in N-concentration indicated that waterlogging, in agreement with the conclusions of Huang *et al.* (1995) and Trought and Drew (1980b), significantly inhibited N-acquisition and -transportation in the plants. Similar results

were also reported for waterlogged wheat (Sharma and Swarup, 1989; Steiger and Feller, 1994), barley (Leyshon and Sheard, 1974) and sorghum (Maranville *et al.*, 1986). The decline in P-concentration observed in the whole waterlogged plants (Table 5.4) and increased seedling survival and dry biomass production with foliar P-application (Table 5.8) could suggest that P absorption by roots and transportation under waterlogging were significantly suppressed by an O_2 deficiency due to impaired root functioning (Trought and Drew, 1980a) and a lack of energy for ion uptake (Barrett-Lennard *et al.* 1990). Increased P-concentrations in the straw and grain at maturity in waterlogged plants (Table 5.4) would indicate that P dilution by photosynthates was very low due to significantly low dry matter accumulation and its partitioning to the grain.

Potassium and sodium concentrations and uptake:

The effect of waterlogging on straw and grain Na-concentration (Table 5.6) and all uptake and concentration parameters of K and Na (Table 5.7) depended on the differences among the wheat genotypes studied. Straw K-concentration declined progressively with increased waterlogging severity for all genotypes except for PRL/Sara and Ducula for which the concentration was slightly increased by the TWI-treatment. Increasing severity in waterlogging, led to lower K-uptake for the sensitive Et-13 and K6290-bulk than for other genotypes. Huang *et al.* (1995) also reported lower stem K-concentrations for sensitive than for tolerant genotypes in response to waterlogging. Trought and Drew (1980b) ascribed low nutrient uptake and transportation through waterlogged roots as the cause for reduced K-accumulation in plants. Waterlogging decreased the grain Na-concentration for Ducula only while it increased for all other genotypes (Table 5.6). Waterlogging generally enhanced whole plant and straw Na-uptake for all genotypes, but the uptake for the TWI-treatment was greater for Et-13 and K6290-bulk than for other genotypes. All parameters of K- and Na-concentration and uptake (except whole plant K- concentration and straw K-uptake) were significantly different among genotypes (Tables 5.4 and 5.5). Waterlogging significantly affected all the uptake and concentration parameters of K and Na (Tables 5.4 and 5.5). All Na-parameters were progressively and significantly increased and the

K-parameters were significantly decreased as waterlogging severity increased. Whole plant K- concentration, measured at anthesis for waterlogged plants, was also lower than the "critical" value (Table 5.9). Waterlogged plants in this study were therefore deficient in K, which is in agreement with previous reports on wheat (Trought and Drew, 1980b; Sharma and Swarup, 1989; Stieger and Feller, 1994; Huang et *al.*, 1995), barley (Drew and Sisworo, 1979; Leyshon and Sheard, 1974), and on sorghum (Maranville *et al.*, 1986). Increased vegetative biomass, straw and grain Na-concentrations and -uptakes by waterlogged wheat were also reported by Sharma and Swarup (1989). Although waterlogging enhanced the concentration of Na in the plant (Tables 5.4 ad 5.5) and in the soil (Table 5.2), it was far below the 17 mg /g dry matter reported by Sharma and Swarup (1988) at an ESP of 32, which caused a 15.7% yield reduction in waterlogged wheat.

Table 5.8. Mean effects of selected nutrient spray on waterlogged durum wheat seedling survival, percentage leaf chlorosis and dry biomass yield, 1999

Factor	Seedlings with green leaves (no./pot)	Chlorosis (%)	Dry biomass (g/pot)
Control	0.00c[+]	88.33a	1.33e
Zn- soil incorporated	1.33b	76.67b	2.27de
Zn spray	3.33a	60.00d	4.10abc
Cu spray	3.67a	43.33fg	5.20ab
P spray	3.67a	70.00c	3.25cd
Zn + Cu spray	4.00a	40.00g	5.62a
Zn + P spray	3.67a	55.00e	3.64bcd
Cu + P spray	3.67a	58.33de	3.44bcd
Zn + Cu + P spray	4.00a	45.00f	4.25abc
P-level	***	***	**
LSD (0.05)	0.97	4.64	1.78
Mean	3.04	59.63	3.68
C.V. (%)	13.90	4.49	17.91

, * Represent significance at the probability levels of 0.01 and 0.001, respectively. [+]Means followed by the same latter are not significantly different at 0.05 probability level.

Table 5.9. Measured, critical and optimal concentration values of mineral nutrients in wheat.

Nutrient	Measured at anthesis			Critical value* (at booting stage)	Optimal range** (at anthesis)
	Free drainage	Transient waterlogging	Continuous waterlogging		
	(%)				
N	2.08	1.67	1.13	2.60	2.80-4.60
P	0.16	0.14	0.10	0.30	0.25-0.59
K	2.12	1.51	1.28	1.80	3.50-5.20
Ca	0.12	0.12	0.14	0.25	0.30-1.08
Mg	0.18	0.17	0.19	0.15	0.08-0.24
Cu	0.55	0.55	0.46	0.50	0.50-1.60
Zn	1.48	0.80	0.68	1.50	2.20-7.0
Mn	2.06	2.91	4.01	3.00	3.00-15.00
Fe	14.98	14.26	18.71	2.50	5.00-18.00

*Melsted et al. (1969)

**Bergmann (1992)

Calcium and magnesium concentrations and uptake:

The effect of waterlogging on Ca- and Mg-concentrations (except for the grain) and-uptake (except the straw Mg) depended on genotypes as indicated by significant interactions between waterlogging and genotypes (Tables 5.6 and 5.7). As waterlogging severity increased, there was a decrease in the whole plant Ca- and Mg- concentrations for K6290-bulk while there was an increase in Ca-concentration for all other genotypes and Mg-concentration for Et-13, PRL/Sara and Ducula with no appreciable change for the other genotypes. Waterlogging significantly increased straw Ca- and Mg-concentrations for all genotypes. The increment in Ca-concentration was the highest for PRL/Sara and in Mg-concentration was the highest for Et-13 and PRL/Sara. Grain Mg-

concentration increased significantly for PRL/Sara and Ducula with no appreciable effect in most other genotypes, as waterlogging severity increased. Straw Ca-uptake increased for all genotypes except for Et-13 under the CWl- treatment. Grain Ca-uptake increased for all genotypes except for K6290-bulk in the TWl- treatment, but it was significantly depressed under CWl. Grain Mg-uptakes were reduced for all genotypes, but the magnitude of reduction was higher for Et-13 and K6290-bulk than for the other genotypes. Huang *et al.* (1995) reported a reduction in leaf Mg-concentration due to waterlogging for a sensitive genotype while there was no effect for a tolerate wheat genotype. Genotypes differed significantly in Ca- and Mg-concentration and uptake parameters except for straw and grain Ca-uptake (Tables 5.4 and 5.5). A significant waterlogging effect was observed for most Ca- and Mg-concentration and -uptake parameters (Tables 5.4 and 5.5). When the whole plant Ca- and Mg-concentrations were compared with the "critical" and "optimum" range values reported for wheat, the Mg-concentrations exceeded the "critical" value but fell within the "optimum" range. Ca-concentrations for all treatments were below the "critical" value (Table 5.9). Several investigators (Huang *et al.*, 1995; Kozlowski 1984; Trought and Drew, 1980b) have concluded that Ca- and Mg- accumulation and -uptake by plants are the least of all the macronutrients affected by waterlogging.

CONCLUSIONS

Waterlogging treatments significantly reduced vegetative dry biomass, straw and grain yields for all genotypes, but to a greater extent for the sensitive Et-13 and K6290-bulk. Root zone oxygenation was significantly depressed by the waterlogging treatments as indicated by lower redox potentials. Soil waterlogging increased all mineral nutrient concentrations in the soil, but the effect was more pronounced for Fe, Mn, K and Na. Nutrient concentration and uptake of wheat under different waterlogging regimes differed among genotypes. Although there was no clear trend for Ca and Mg, sensitive genotypes accumulated more Fe, Mn, and Na and less Cu, Zn, K, P and N than the tolerant genotypes. Concentrations of the latter nutrients appeared to be lower than the

"critical" values previously reported for wheat. Increases in the number of seedlings with green leaves, dry biomass yield and lower percentage leaf chlorosis were observed when waterlogged wheat seedlings received foliar nutrient application of Cu, Zn, and P. This implied that there was a nutrient-induced improvement in waterlogging tolerance and, therefore, the adverse effects of waterlogging could be offset to some extent by the foliar application of deficient nutrients. The results indicated that the damaging effects of waterlogging on wheat were not due to Fe, Mn, or Na toxicity but can rather be attributed to a decreased nutrient uptake due to O_2 deficiency in the root zone, resulting in particularly P- and Zn-deficiencies. Zn-deficiency is most common in cool and wet highland Vertisols with high montmorillonite clay contents, pH-values, and high phosphate and organic matter contents. In a breeding program aimed at improving waterlogging tolerance in wheat, selection of genotypes with greater ability to overcome the waterlogging–induced nutrient deficiencies, particularly P- and Zn-deficiency could improve wheat productivity on waterlogged soils. Further studies are, however, necessary to clearly define the effect of P and Zn nutrition on the reduced growth resulting from waterlogging and also to establish the mode of genetic inheritance of tolerance to P- and Zn-deficiencies, associated with waterlogging in wheat.

CHAPTER VI

DIALLEL ANALYSIS OF WATERLOGGING STRESS TOLERANCE IN WHEAT (*TRITICUM AESTIVUM* L.)

ABSTRACT

Wheat (*Triticum aestivum* L.) genotypes differ in their tolerance to waterlogging stress. Very little information is available, however, about the genetic system governing the inheritance of waterlogging stress tolerance. This study was undertaken to assess the combining ability effects, variance components, heterotic responses, heritability and correlations of waterlogging tolerance in a diallel cross involving five diverse bread wheat genotypes with contrasting tolerance response to waterlogging stress. Two separate greenhouse pot experiments, freely drained (FD) and continuously waterlogged for seven weeks (CWl), were conducted in 1999/2000 using both the parents and F_1s, excluding reciprocals. A separate statistical analysis of measurements was performed for each experiment.

The results showed that genotypic variability accounted for most of the variation among genotypes studied. The average performance of genotypes and the magnitude and the direction of most estimates varied considerably between the two experiments. Highly significant general combining ability (GCA) and specific combining ability (SCA) were observed for all characteristics studied except GCA effects for total grain yield (GYt) in the FD- and grain yield from tiller spikes (GYts) in both experiments, and SCA effects on spikelets per spike (SlPS) and green leaf number (GLN) in the FD- and plant height (PH) and stress susceptibility index (SSI) in the CWl-experiments. A comparison of their relative magnitudes indicated that GCA effects were more important than SCA effects for most characteristics studied in both experiments. However, preponderance of SCA effects was also observed on productive spikes (PS) and days to heading (DH) in the CWl- and for GYts in both experiments. Relatively high estimates of heritability and predictability ratios were also observed for most characteristics relevant to waterlogging stress tolerance, confirming the importance of both additive and non-additive gene effects in controlling the waterlogging tolerance among the genotypes studied. The

degree of dominance for waterlogging tolerance characteristics was estimated to be in the partial and complete dominance range.

Under waterlogging conditions, GYt correlated genotypically and phenotypically positively with all its components, biomass yield (BY), PH, days to heading (DH), GLN and stress tolerance index (STI) and negatively with chlorosis (CHl), area under chlorosis progress curve (AUCPC-value) and SSI index. Substantial mid- and high-parent heterotic responses were observed for most characteristics in some crosses, but the extent of heterosis expression for most characteristics in some crosses were higher in the CWl- than in the FD- experiment.

From the results, it is suggested that the best combining genotypes, PRL/SAR and Ducula, for waterlogging tolerance, may be used to initiate a short-term breeding program to improve waterlogging tolerance in wheat. The most useful improvements in the waterlogging stress tolerance of wheat would, however, be attainable with a breeding strategy that could in the tong tem exploit both additive and non-additive gene effects simultaneously.

Key words: Heritability; heterosis; combining ability; correlation; waterlogging tolerance, variance components; wheat

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INTRODUCTION

Much of the world's wheat is grown in the marginal agricultural zones, where yield is often affected by drought or waterlogging stress (Briggle and Curtis, 1987). Waterlogging stress has been shown to have substantial adverse effects on growth and yield of wheat in many high rainfall regions of the world (Watson *et al.*, 1976; Cannell *et al.*, 1980; Belayneh, 1986; Grieve *et al.*, 1986; Sharma and Swarup, 1989; Musgrave and Ding, 1998;). In the central and eastern highland regions of Africa, the incidence of

waterlogging on wheat production is more pronounced because of the widespread occurrence of poorly drained heavy black clay Vertisols (Jutzi and Abebe, 1986; Coulombe *et al.*, 1996) and low evaporative demand during the crop growing season (Semane *et al.*, 1999). To improve wheat production in these regions of Africa, development of cultivars that are tolerant to waterlogging stress appear to be an important objective for wheat breeders. Studies have shown the presence of wide genetic variability for tolerance to waterlogging stress in wheat (Davies and Hillman, 1988; Thomson *et al.*, 1992; Gill *et al.*, 1992, 1993; Van Ginkel *et al.*, 1992; Gardner and Flood, 1993; Cai *et al.*, 1994; Cao and Cai, 1991; Lin *et al.*, 1994; Musgrave and Ding, 1998). Nevertheless, the inheritance of waterlogging tolerance has not been extensively studied (Cao *et al.*, 1994; Cao *et al.*, 1995; Boru, 1996). Knowledge of the genetic systems of waterlogging tolerance stress in wheat will increase efficiency in breeding waterlogging tolerant varieties. The nature of the genetic mechanisms involved in waterlogging tolerance can be revealed through the application and analysis of suitable genetic designs.

The diallel cross is defined as making all possible crosses among a group of genotypes (Dudley and Moll, 1969). Diallel analysis as described by Griffing (1956) is a systematic method of evaluating populations or a group of genotypes in hybrid combinations. This analysis has been widely used by plant breeders to determine the genetic parameters of different characteristics in reference populations and evaluate parental genotypes in order to efficiently identify the average performance of crosses (Dudley and Moll, 1969; Wilson *et al.*, 1978; Baker, 1978; Cukedar-Olmedo *et al.*, 1997; Saghroue and Hallauer, 1997). Estimates of breeding values of parents and the type of gene action, obtained from the combining ability analysis in a diallel crossing system (Griffing, 1956; Dudley and Moll, 1969; Wright, 1985), have been largely used in wheat as a guidelines in parental selection (Grant and McKenzie, 1970; Bhatt, 1971; Wilson *et al.*, 1978; Gallais, 1988; Singh *et al.*, 1988; Mandal and Maity, 1992; Srivastava *et al.*, 1992; Ronga *et al.*, 1997). Information on the type of gene action and estimates of various genetic parameters of characteristics for a population can be very useful to plant breeders in defining the appropriate breeding methodologies and strategies that will effectively utilize the genetic variance present in the development of

germplasm targeted to overcome specific production constraints (Griffing, 1956; Gardner and Eberhart, 1966; Singh and Chaudhary, 1979). The choice of parents can also be greatly facilitated by correlation analysis of parents and their respective progenies (Cox and Frey, 1984). Estimates of variance components can be used to calculate heritabilities, genetic correlations and predicted gains from selection (Singh and Chaudhary, 1979; Falconer and Makey, 1996; Saghraue and Hollauer, 1997).

A diallel crossing system has been used to estimate combining ability effects of salinity tolerance (Singh *et al.*, 1988; Kathiria and Sharma, 1996), boron toxicity tolerance (Mandal and Maity, 1992) and high temperature tolerance (Pathak and Nema, 1988; Celliers *et al.*, 1999) and water stress tolerance (Sinolinding and Chowdhry, 1974; Pathak and Nema, 1988) in wheat. A diallel analysis has also been employed in studies of submergence tolerance in rice (Haque *et al.*, 1989) and pre-germination flooding tolerance in sorghum (Thseng and Hou, 1993). Very few studies with limited genetic analysis have been reported on the inheritance of waterlogging tolerance in wheat (Cao *et al.*, 1994; Cao *et al.*, 1995; Boru, 1996).

The objectives of this study were: i) to estimate combining ability effects and genetic parameters of waterlogging tolerance and associated agronomic characteristics under free drainage and waterlogging conditions; ii) to determine heritabilities as well as phenotypic and genotypic correlations of waterlogging tolerance and major agronomic characteristics of wheat under free drainage and waterlogging conditions; iii) to estimate both mid- and high-parent heterosis for various characteristics of wheat under free drainage and waterlogging conditions; and iv) to assess the relationship between heterotic response and genetic diversity of parents.

MATERIALS AND METHODS

Parents and F_1 hybrids:

Five diverse bread wheat genotypes, three tolerant and two sensitive to waterlogging stress were selected as parents for a diallel cross. Details of parental lines regarding

their reaction to waterlogging stress, pedigree/cross and place of origin are given in Table 6.1. The diversity of parental genotypes as measured by coefficients of parentage and seed storage protein markers are presented in Table 6.2. The parents were hand emasculated and pollinated to produce all possible combinations of F_1 hybrid seeds. The crosses were made in the 1998/99 summer in a greenhouse at the Free State University, South Africa. The 10 F_1 populations (excluding the reciprocals) and the five parents were tested for the waterlogging stress tolerance in 1999.

Experimental Design:

Two sets of separate pot experiments, freely drained (FD) and continuously waterlogged for seven weeks (CWl) were laid out side-by-side under controlled conditions in a greenhouse. Both experiments were arranged in randomised complete block design (RCBD). Each experiment consisted of 15 entries (five parents and 10 single crosses) and four replications. This design was chosen, as it is most commonly applicable for diallel study (Griffing, 1956; Dudley and Moll, 1969).

Table 6.1. Description of parental lines used in a 5 x 5 diallel cross for the inheritance study of waterlogging tolerance

Parental line	Source	Cross/pedigree	Reaction to waterlogging
ET 13 (Et)	Ethiopia	UQ105 Sel. x ENKOY	Susceptible
K 6290-Bulk (Bulk)	Ethiopia	(AF.MAYO x GEM) x Romany B.C.	Susceptible
Vee/Myna	CIMMYT	KVZ/BUHO//KAL/BB/5/ND/WW//LEE/FN/3/N/4/TI-R	Tolerant
PRL/Sara	CIMMYT	FKN/3/2*FCR//KAD/GB54/4/BB/CHA/6/T_AST/4/TP// CNO67/NO/3/CNO67/7C/5/JUP	Tolerant
Ducula (x1)	CIMMYT	HUC/TI-R/3/ATR*2/7C//NAC/4/SARA	Tolerant

Conduct of the pot experiment:

The soil type used was Vertisol with 3.2% organic matter and 46% clay content. The soil was pulverized and sieved to remove clogs and fibrous root materials, thoroughly mixed with nutrient solution applied at a rate of 70 mg N as KNO_3 and 35 mg P as

K_2HPO_4 kg^{-1} soil, then used to fill a three litre size polyethylene pots, perforated at the bottom. Eight seeds of each genotype were planted per pot on 22 March 1999, covered slightly with a thin-layer of loose soil, and then thinned to four seedlings after full emergence. For CWl experiments, pots containing seedlings were put into an unperforated five-litre size pot, and then waterlogging with tap water was initiated when seedlings reached four-leaf stage. Waterlogging levels were maintained at 2-3 cm above the soil surface by watering daily for seven weeks. In both experiments, plants were supplied with 0.5 mg N nutrient solution from NH_4NO_3 at two weeks intervals. Greenhouse temperatures were maintained at 15°C minimum and 25°C maximum, respectively.

Measurements

During waterlogging treatment, the number of total (TLN) and green leaf numbers (GLN) per four main plants in both experiments were counted every week and seedling height as a distance in cm from soil surface to the tip of the youngest leaf, was also measured every week in both experiments. The seedling height measurements were further used to calculate seedling shoot elongation rate (SER: cm day^{-1}) for each genotype. In waterlogged experiments, percentage chlorosis (Chl) was recorded weekly, from which area under chlorosis progress curve (AUCPC) was determined using the formula: $AUCPC = \sum_{i}^{n-1}\left(\frac{x_i + x_{i+1}}{2}\right)\left(t_{i+1} - t_i\right)$ (Campbell and Madden, 1990), where n is the number of assessment times for percentage leaf chlorosis x at time t. In both experiments, days to heading (HD) were recorded as the number of days from planting to 50% ear emergence. At maturity, the number of productive spikes per pot (PS), the number of spikelets per spike (SlPS) as well as plant heights (PH), as a distance in cm from soil surface to the tip of awns were determined, in both experiments. All plants were cut at the soil surface to determine biomass yield (BY). Heads were separated in to main spikes and tiller spikes and hand threshed separately, then the resulting grains were weighted to determine grain yield main $spikes^{-1}$ (GYms) and tiller $spikes^{-1}$ (GYts), respectively. Total grain yield per pot was determined as sum of GYms and GYts and the total number of grains pot^{-1}(TNG) were determined by summing up the number of grains from each of the main spikes (GNms) and tiller plant spikes (GNts). Kernel mass

(KM: mg kernel^{-1}:) and number of grains per spike (GPS) was determined by dividing GYt by TNG and TNG by PS, respectively. The number of grains spikelet^{-1} (GPSl) was calculated as GPS/SlPS. Yield based indices such as the stress susceptibility index (SSI) (Fischer and Maurer, 1978) and stress tolerance index (STI) (Fernandez, 1992) were calculated using the formula: $SSI = \left(Y_{FD} - Y_{CWI}\right) / \left(Y_{FD} * \left(1 - \left(\bar{Y}_{CWI} / \bar{Y}_{FD}\right)\right)\right)$ and $STI = \left[\left(Y_{FD}\right)\left(Y_{CWI}\right)\right] / \left(\bar{Y}_{FD}\right)^2$, where Y_{FD} and Y_{CWI} are yields of a genotype under free drainage and continuous waterlogging experiments, respectively, $\bar{Y}_{FD}$ and $\bar{Y}_{CWI}$ are mean yields of all genotypes under free drainage and continuous waterlogging experiments, respectively.

Statistical analyses:

Analysis of variance: All measured characteristics were subject to the analysis of variance using *AGROBASE™* software (Argonomix software Inc., Canada) to assess the performance of genotypes under freely drained and waterlogged conditions. Data were analysed separately for each set of experiment. Mean squares were compared with F-values to assess the significance of the difference among genotypes. In addition, single degrees of freedom contrasts between parents and F_1s, waterlogging sensitive (SP) and tolerant parents (TP), (SxS) vs (SxT) F_1s, (SxS) vs (TxT) F_1s, and (SxT) vs (TxT) F_1s were made using GLM procedure of the SAS statistical package (SAS Institute, Cary, NC).

Analysis of combining ability: Following the detection of a significant F-value for the genotypes, a separate combining ability analysis for each experiment was performed using both parents and F_1 generations (excluding the reciprocals) by Method II, Model I of the diallel cross analyses provided by Griffing (1956), assuming fixed effects for genotypes. General combining ability (GCA) effects and specific combining ability (SCA) effects were estimated for all measured characteristics in both experiments. The ratio between GCA and SCA mean squares were also performed to determine the relative magnitude of mean squares due to GCA and SCA. The significance of GCA and SCA values were determined by t-test using gi and sij variances, respectively (Griffing, 1956; Singh and Chaudhary, 1979).

Analysis of genetic components: To determine the relative contribution of genetic components, a random effect model (i.e., Griffing's Model II) was used to obtain estimates of GCA variances $(\delta^2 gca)$ and SCA variances $(\delta^2 SCA)$ for each character. Variances for these estimated components were calculated as outlined by Singh and Chaudhary (1979) and Wricke and Weber (1998). Additive variance (V_A) and dominance variance (V_D) were estimated as $V_A = 2\delta^2 gca$ and $V_D = \delta^2 sca$, respectively. Genotypic variance (V_G) and dominance variance (V_D) were estimated as $V_G = V_A + V_D$ and $V_P = V_G + V_E$, respectively. The relative sizes of variances due to GCA and SCA were compared following Baker's predictability ratio (PR): $PR = \frac{2\delta^2 gca}{(2\delta^2 gca + \delta^2 sca)}$ (Baker, 1978). The closer this ratio is to unity, the greater is the predictability of F_1 progeny performance based on the general combining ability effects alone. Estimation of the degree of average dominance $\sqrt{\frac{H}{D}} = \sqrt{\left(\frac{\delta^2 sca}{\delta^2 gca}\right)}$ was made following Singh and Chaudhary (1979). Both broad $(h^2 b)$ and narrow sense $(h^2 n)$ heritabilities were calculated as $h^2 b = \frac{V_G}{V_P}$ and $h^2 n = \frac{V_A}{V_P}$, respectively.

Heterosis estimates: Heterosis was estimated in two ways: The true heterosis (mid-parent heterosis: MPH) was expressed as a percent of the mid-parent value: $MPH = \left(F_1 - MP / MP\right) \times 100$. To understand the magnitude of hybrid performance in relation to its genetic potential, high-parent heterosis (HPH) was calculated as percent of high-parent value: $HPH = \left(F_1 - HP / HP\right) \times 100$. Significance of MPH and HPH values were determined by single degrees of freedom contrasts between F_1 generations and mid- and high-parent values, using the GLM procedure of the SAS statistical package (SAS Institute, Cary, NC).

Genetic distances: Genetic relationships among parental lines were determined using pedigree information and electrophoretic composition of the three major seed storage proteins. Coefficients of parentage (r) were computed for all 10 pairs of the five parental lines according to the method and assumptions described by Cox *et al.* (1985b). The coefficients were calculated using WCOP procedure of IWIS computer package (Skovmand *et al.*, 2000). Genetic distances were then computed as 1-r. Three major seed storage proteins (gliadins, high and low molecular weight glutenin subunits) were determined for all five parental genotypes using SDS-PAGE system described in Chapter III. Polymorphic protein bands were scored as present (1) or absent (0), then used to calculate genetic distances (GD-SSP) using Euclidean method of NCSS computer program (Hintze, 1998).

Table 6.2. Estimates of mean genetic distances of wheat parental lines from protein markers (upper diagonal) and coefficients of parentage (1-r) (lower diagonasl)

Parent	ET-13	K6290-Bulk	Vee/Myna	PRL/Sara	Ducula
ET-13	-----	0.623	0.651	0.574	0.660
K6290-Bulk	0.980	-----	0.623	0.642	0.614
Vee/Myna	0.937	0.982	-----	0.651	0.660
PRL/Sara	0.938	0.988	0.843	-----	0.711
Ducula	0.944	0.988	0.843	0.648	-----

Correlations: A correlation is the ratio of the appropriate covariance to the root of the product of the variances of the two traits (Falconer and Makey, 1990). For each trait in both experiments, Spearman rank correlations were calculated among F_1 hybrid performance and SCA effects of crosses with genetic distance estimates determined based on pedigree information (1-r) and seed storage information (GD-SSP). Rank correlation was performed using NCSS 2000 computer package (Hintze, 1998). Genotypic and phenotypic variances and covariances (Singh and Chaudhary, 1979)

were estimated using the output from *SAS* multivariate analysis (MANOVA) procedure (SAS Institute, Cary, NC). Phenotypic (r_p) and genotypic (r_g) correlations were calculated using the formula: $r_p = \frac{\delta_{pxy}}{\sqrt{\delta^2_{px} \times \delta^2_{py}}}$ and $r_g = \frac{\delta_{gxy}}{\sqrt{\delta^2_{gx} \times \delta^2_{gy}}}$, respectively (Falconer and Makey, 1996; Griffing, 1956). Where δ_{pxy} and δ_{gxy} are phenotypic and genotypic covariance, δ^2_{px} and δ^2_{py} are phenotypic variances and δ^2_{gx} and δ^2_{gy} are genotypic variances of trait x and y, respectively. The significance of the correlation coefficients was determined using the student's t-test (Steel and Torrie, 1980): $t = r / \sqrt{1 - r^2 / n - 2}$, where r is the correlation coefficient and n is the number of observations.

RESULTS AND DISCUSSION

Analysis of variances:

Mean squares of various characteristics with their corresponding means and coefficients of variability (CV) from the separate analysis of variance for the two experiments are presented in Table 6.3. Genotype performance for various characteristics was substantially more reduced in the CWl- than in the FD-experiment as shown by large differences in the mean squares and mean values of various characteristics studied. Experimental variability was higher in CWl- than in the FD-experiment as indicated by CVs, which for different characteristics ranged from 4.1 to 39.3% in the CWl-experiment and from 3.5 to 17.0% in the FD-experiment. In CWl-experiment, six of the 18 characteristics had CV < 10% and three > 20%, while in the FD-experiment, all characteristics had CV < 17%. Stress environments are usually characterized by larger environmental variances than the optimum environments (Ceccarelli *et al.*, 1991).

In both experiments, the analysis of variance showed significant variation among the 15 genotypes for all measured characteristics except for GYts in the FD-experiment (Table 6.3). Significant differences were found among parents, crosses (F_1s), and between

waterlogging-sensitive (SP) and –tolerant parents (TP) and F_1s and parents for most of the characteristics studied in both experiments. Comparisons of contrasts between the SxS vs SxT, SxS vs TxT and SxT vs TxT F_1s exhibited significant differences for most of the characteristics studied in both experiments, but the magnitude of differences for most characteristics were higher in the CWl- than in the FD-experiments. These results indicated the presence of genetic variability for various characteristics under both experimental conditions and therefore suggested that detailed analysis of gene action and combining ability was warranted.

Combining ability components:

Combining ability effects quantitatively measure the comparative performance of parents and cross combinations in relation to one another. Mean squares of the analysis of the components of combining ability for various characteristics measured in both experiments are shown in Table 6.4. Significant GCA mean squares were found for all measured characteristics and yield-based indices except for GYt and GYts in one or both experiments. Mean squares due to SCA were also significant for most characteristics and STI index except for KM, SlPS and PH in CWl- and for SlPS and GLN in the FD-experiments as well as for SSI index. The magnitude of mean squares of the components for various characteristics varied between the two experiments, indicating the presence of variability in the genetic expression of characteristics under the two contrasting experimental conditions. The mean squares of GCA for GYt, GYms, KM and GPSl were higher in the CWl- and that of BY, GPS, PS, PH, DH, SER and TGN were higher in the FD-experiment, where as the GCA mean squares for GYts, SlPS and GLN were comparable in both experiments. The SCA mean squares of all characteristics were higher in the FD-experiment except for KM, PS, and SlPS. The magnitudinal differences between the two experiments observed in this study are in agreement with the findings of other workers (Singh *et al.*, 1986; Singh, 1988; Mandal and Maity, 1992; Srivastava *et al.*, 1992) who noted the importance of environmental factors in the genetic expression of characteristics in wheat. Singh *et al.* (1986) observed large differences in both GCA and SCA mean squares for several characteristics of wheat measured under normal and stress growth environments.

The relative importance of combining ability components:

The relative importance of GCA and SCA for each of the characteristics studied in both experiments and indices are presented in Table 6.4. The GCA/SCA ratio was higher than unity for the 14 of the 16 measured characteristics in the CWl-experiment, 10 of the 14 characteristics in the FD-experiment as well as for the two yield-based indices, indicating the importance of the GCA component in the inheritance of waterlogging tolerance characteristics and most other agronomic characteristics. The relative contribution of GCA for BY, GPS, KM, SlPS, PH, DH, SER, TLN and GLN in both experiments, GYt, GYms, GPSl, Chl and AUCPC-value in the CWl- experiment and for SSI and STI indices was higher than the relative contribution of SCA and always larger than 50%. The relative importance of SCA for GYt, and GPSI in the FD-experiment, PS in the CWl-experiment, and for GYts in both experiments was higher than the contribution of GCA and larger than 50%. The relative importance of both GCA and SCA for GYms in the FD-experiment were nearly equal to 50%. The results of this study indicated that, although the relative importance of both GCA and SCA varied between the two experiments and across characteristics, GCA contribution was generally higher than SCA in the genetic expression of waterlogging tolerance and most other agronomic characteristics under the free drainage and waterlogging conditions.

Table 6.3. Analysis of variance for various characteristics of wheat genotypes in the free drainage and waterlogging greenhouse pot experiments in 1999/2000

Character	Exper-iment	Sources of variation							Mean	C.V. (%)
		Entry (14)	SP vs.TP(1)	P vs F_1 (1)	(SxS)F_1 vs. (SxT)F_1(1)	(SxS)F_1 vs. (TxT)F_1(1)	(SxT)F_1 vs. (TxT)F_1(1)	Error (42)		
Gyt(g/pot)	FD	29.239**	0.280ns	87.38**	0.015ns	4.941ns	14.58ns	11.452	30.37	11.14
	CWI	19.776***	88.58***	30.00***	52.483***	20.94**	12.92*	2.065	10.94	13.14
Gyms (g/pot)	FD	16.945***	26.13***	59.94***	4.734ns	0.993ns	24.50***	1.374	12.76	9.18
	CWI	10.261**	43.56	14.214***	23.48***	44.66***	12.33***	0.673	5.98	13.71
GYts (g/pot	FD	14.476ns	21.68ns	0.208ns	4.180ns	1.505ns	1.253ns	8.973	17.61	17.01
	CWI	9.050***	7.450ns	2.730ns	5.537ns	4.688ns	50.84***	2.155	4.96	29.59
BYM (g/pot)	FD	174.81**	534.67***	10.208ns	0.005ns	14.19ns	39.161ns	52.861	66.95	10.86
	CWI	68.332***	69.616ns	143.01*	298.13***	441.65***	63.094ns	19.842	33.24	13.40
GPS (no.)	FD	492.47***	1296.9***	73.164ns	133.22ns	54.40ns	31.21ns	60.315	48.41	16.04
	CWI	159.65***	117.41*	59.64ns	46.94ns	461.28***	605.52***	16.859	23.67	17.35
KM(m/grain)	FD	103.77***	0.001ns	514.60***	14.18ns	10.175ns	0.294ns	15.394	52.43	7.48
	CWI	228.96***	766.59***	1242.9***	468.***	708.40***	108.05**	14.228	42.53	8.87
PS(no./pot)	FD	19.600***	95.408***	33.08**	10.50ns	11.02ns	0.222ns	3.578	12.65	14.95
	CWI	22.445***	11.408ns	5.633ns	12.59§	30.08**	206.72***	3.252	10.99	16.42
SIPS (no.)	FD	210.35***	177.633*	57.18ns	143.01*	114.08ns	0.681ns	32.794	81.53	7.02
	CWI	229.34**	464.133***	2.700ns	143.01*	114.08ns	0.681ns	34.643	60.20	9.78
GPSl (no.)	FD	0.428***	1.267**	0.525*	0.003ns	0.309ns	0.675*	0.104	2.92	11.06
	CWI	0.256***	0.833***	0.030ns	0.180*	0.241*	0.023ns	0.035	2.14	8.71
PHm (cm)	FD	447.23***	1620.7***	800.83***	238.10**	1950.8***	2357.6***	23.085	113.0	4.25
	CWI	222.89***	504.30***	276.03***	42.00ns	252.08**	256.89**	30.933	97.13	5.73
DH (no.)	FD	798.20***	67.50***	2253.33***	233.36***	1776***	2069***	6.498	73.83	3.45
	CWI	218.45***	0.075ns	546.13***	6.482ns	150.52*	572.36***	21.979	80.93	5.79
SERcm/day)	FD	0.789***	2.315***	1.395***	0.883***	4.527***	4.158***	0.007	1.05	8.10
	CWI	0.189***	0.407***	0.359***	0.156***	0.860***	0.828***	0.009	0.72	13.33
TLN(no./ 4MP)	FD	128.27***	440.83***	130.21***	2.88ns	238.52***	773.57***	13.385	44.92	8.15
	CWI	70.02***	124.03***	99.01***	59.52***	315.19***	296.06***	4.518	43.48	4.89
GLN(no./ 4MP)	FD	55.27***	182.53***	38.53ns	10.500ns	36.75ns	220.50	10.429	23.07	14.00
	CWI	51.39***	346.80***	7.008ns	130.38***	238.5***	60.50***	2.979	11.62	14.86
Chl (%)	CWI	1583***	12161***	1936***	6550***	6098***	15.125ns	74.098	36.77	23.41
AUCPC-value	CWI	48189***	3462562***	648270***	1871359***	2099197***	76375ns	29279	913.2	18.74
SSI		0.040***	0.255***	0.011ns	0.128**	0.083**	0.006ns	0.011	0.99	10.55
STI		0.035***	0.089***	0.087***	0.064***	0.021*	0.023*	0.004	0.36	17.08

FD=free drainage; CWI= continuous waterlogging for 7 weeks; GYt= total grain yield; GYms= grain yield main plant spikes^{-1}; GYts= grain yield tiller plant spikes^{-1}, BY= biomass yield at maturity; GPS= grains spike^{-1}, KM= grain mass; PS= productive spikes; SIPS=spikelets spike^{-1}; GPSl= grains spikelet^{-1}, PH= plant height, DH= days to heading, SER= Shoot elongation rate; TLN= total leaf number; GLN= green leaf number; Chl= chlorosis, AUCPC-value = Area under chlorosis progress curve; SSI= stress susceptibility index; STI stress tolerance index; SP= susceptible parent; TP= tolerant parent; SxS =crosses between SPs ; SxT= crosses between SP and TP; TxT= crosses between TPs; Numbers in parenthesis represent degrees of freedom; *,**,*** significant at the probability levels of 5, 1 and 0.1%, respectively.

Table 6.4. Mean squares and relative importance of components of combining ability for various characteristics of wheat in the free drainage and waterlogging greenhouse pot experiments in 1999/2000

Character+	Experiment+	Sources of variation			Relative importance		
		GCA (4)†	SCA (10)	Error (42)	GCA/SCA	GCA (%)	SCA (%)
GYt (g/pot)	FD	5.310ns	8.159**	2.864	0.651	39.42	60.58
	CWI	8.927***	3.363***	0.506	2.654	72.64	27.36
GYms (g/pot)	FD	4.418***	4.172***	0.341	1.059	51.43	48.57
	CWI	7.292***	0.667***	0.171	10.933	91.62	8.38
GYts (g/pot	FD	1.015ns	4.681*	2.244	0.217	17.82	82.18
	CWI	1.148ns	2.687***	0.537	0.427	29.93	70.07
BY (g/pot)	FD	61.735**	36.413*	13.238	1.695	62.90	37.10
	CWI	33.111***	10.718*	4.977	3.089	75.37	23.92
GPS (no.)	FD	343.047***	35.117*	15.090	9.768	90.72	9.39
	CWI	113.424***	10.566*	4.218	10.735	91.48	8.52
KM (mg/grain)	FD	51.997***	15.506***	3.842	3.353	77.03	22.97
	CWI	109.116***	36.440***	3.555	2.994	74.96	25.04
PS (no./pot)	FD	12.253***	1.959*	0.895	6.255	86.22	13.78
	CWI	4.494**	6.058***	0.813	0.742	42.59	57.41
SIPS (no.)	FD	169.788***	5.708	8.198	29.746	96.75	3.25
	CWI	156.725***	17.575ns	8.661	8.917	89.92	10.08
GPSI (no.)	FD	0.079*	0.118***	0.026	0.669	40.10	59.90
	CWI	0.174***	0.022*	0.009	7.909	88.78	11.22
PH (cm)	FD	298.396***	37.173***	5.771	8.027	88.92	11.08
	CWI	160.015***	14.005	7.733	11.426	91.95	8.02
DH (no.)	FD	275.071***	169.342***	1.624	1.624	61.90	38.11
	CWI	108.101***	33.215***	5.495	3.255	76.50	88.91
SER (cm/day)	FD	0.529***	0.066***	0.002	8.015	86.03	13.97
	CWI	0.117**	0.019***	0.002	6.158	88.07	11.93
TLN (no./ 4 MP)	FD	83.853***	11.355**	3.346	7.385	85.07	14.93
	CWI	42.583***	7.473***	1.130	5.698	87.38	12.63
GLN (no./ 4 MP)	FD	35.525***	5.133ns	2.607	6.921	95.05	4.96
	CWI	39.779***	2.074**	0.745	19.180	85.09	14.91
Chl (%)	CWI	962.958***	168.798***	18.524	5.705	85.09	14.91
AUCPC-VALUE	CWI	317247***	41763.5***	7319.725	7.596	89.11	11.63
SSI		0.022***	0.005ns	0.003	4.400	81.48	18.52
STI		0.013***	0.007***	0.001	1.857	65.00	35.00

+See Table 3 for abbreviations. *,**,*** significant at 0.05, 0.01, 0.001 levels of probability, respectively, and ns represents non significance; †the numbers in the parenthesis represent degrees of freedom.

General combining ability (GCA) effects:

The GCA effects are numerical values assigned to the parents according to their average performance in the hybrid combinations. Estimates of GCA effects for various characteristics studied in one or both experiments are presented in Table 6.5. The results revealed that the GCA effects of parents for most characteristics at the two different experiments were variable both in direction and magnitude, reflecting how the genetic expression of parents were sensitive to the stresses caused by soil waterlogging. Similar findings on GCA effect differences were reported for wheat at different levels of boron (Mandal and Maity, 1992), sodicity (Kathiria and Sharma, 1996), sowing dates (Chovata and Jordan, 1989), years (Srivastava *et al.*, 1992) and under irrigated and rainfed conditions (Chowdhury and Dhanda, 1988).

In both experiments, GCA effects of individual parents were significant for most of the characteristics studied, suggesting the presence of adequate diversity in the genetic constitution of parents for most characteristics measured in one or both experiments. The results, however, indicated that none of the parents were good general combiners for all the characteristics studied in both experiments. In the FD-experiment, none of the five parents exhibited significant GCA effects on GYt and GYts. The GCA effects of Ducula and PRL/Sara were positive and significant for SlPS, DH, TLN and GLN; the latter parent also had positively significant GCA effects on GYms, GPS and GPSl. Et-13 exhibited a positive and significant GCA effects on BY, PS, PH, DH and SER. K6290-Bulk also had positively significant GCA values on KM, PH and SER. Vee/Myna exhibited positive and significant GCA value on KM. Moreover, each of the five parents had negatively significant GCA effects in one or more characteristics.

In the CWl-experiment, there was no single parent, which exhibited significant GCA effects on GYts. Of the three tolerant parents, Ducula and PRL/Sara were good general combiners for GYt, GYms, BY, GPS, SlPS, GPSl, DH, TLN and GLN. The former parent also had positive and significant GCA effect on KM and negative values on SER and PS; the latter parent expressed positively significant GCA value on PH and negative values on SER. The GCA effects of Vee/Myna, one of the tolerant genotypes were negatively significant for all characteristics except for KM. The two waterlogging–

sensitive parents, ET-13 and K6290-Bulk were good general combiners for PS and DH, and for PH and SER, respectively, but both parents exhibited negative significant GCA effects on GYt, GYms, BY, GPS, KM, SIPS, GPSl, TLN and GLN; K6290-Bulk also had negative significant GCA effects on PH. The waterlogging-tolerant parents, Ducula and PRL/Sara, had significantly high negative GCA effects for Chl, AUCPC- and SSI-values, and positive GCA values for STI index. On the other hand, waterlogging-sensitive parents, Et-13 and K6290-Bulk, had significant high positive GCA values for Chl, AUCPC and SSI; K6290-Bulk also had negatively significant GCA effect on STI index. Mainly additive gene effects cause significant GCA effects, even though non-additive genes may also be involved (Baker, 1978). Large positive GCA values observed for most characteristics indicate the occurrence of effective transmission of genes for these traits from parents to their progenies. Predominance of positive GCA effects for characteristics relevant for waterlogging tolerance indicated that selection based on the performance of individual lines should be effective in improving waterlogging stress tolerance and yield in the populations tested in this study. Large negative GCA effects for Chl, AUCPC- and SSI-values and positive effects for GLN and STI-value are desirable in the development of waterlogging-tolerant genotypes. Ducula and PRL/Sara were found to be the best general combiners for most characteristics relevant to waterlogging-tolerance and major agronomic characteristics. Therefore, these parents could be used in the development of waterlogging stress tolerant wheat genotypes.

Table 6.5. General combining ability of parental lines for various characteristics of wheat in the free drainage and waterlogging greenhouse experiments in 1999/2000

Character[+]	Exper-iment	Parental lines					SEgca
		ET 13	K 6290-Bulk	Vee/Myna	PRL/Sara	Ducula	
GYt (g/pot)	FD	-0.344	0.713	-1.341**	0.749	0.224	0.57215
	CWI	-0.624*	-1.084 ***	-0.734 ***	1.309 ***	1.134***	0.24043
GYms (g/pot)	FD	-0.761 ***	0.360	-0.883***	0.967 ***	0.317	0.19745
	CWI	-1.079 ***	-0.829 ***	-0.218	0.986 ***	1.139 ***	0.13966
GYts (g/pot	FD	0.429	0.354	-0.461	-0.221	-0.100	0.50636
	CWI	0.479	-0.260	-0.514	0.308	-0.014	0.24769
BY (g/pot)	FD	3.767 **	-0.901	-4.319**	1.260	0.192	1.22999
	CWI	-1.169 *	-2.698 ***	-0.541 ***	1.838 *	2.570 **	0.75421
GPS (no.)	FD	-4.171 **	-1.856	-6.392 ***	11.558 ***	0.861	1.31323
	CWI	-1.906 **	-3.406 ***	-3.396 ***	4.604 ***	4.104 ***	0.69428
KM (mg/grain)	FD	-2.562 ***	2.281 **	2.974 ***	-3.001 ***	0.301	0.66267
	CWI	-4.695 ***	-2.902 ***	2.944 ***	-0.163	4.816 ***	0.63740
PS (no./pot)	FD	1.871 ***	0.014	0.300	-1.807***	-0.379	0.31972
	CWI	0.907 **	-0.214	0.514	-0.200	-1.200 ***	0.30480
SlPS (no.)	FD	-1.777	-1.314	-6.421 ***	6.436 ***	3.079 **	0.96797
	CWI	-4.886 ***	-2.600 *	-2.671 *	5.400 ***	4.757 ***	0.99488
GPSl (no.)	FD	-0.045	-0.026	-0.067	0.188 *	-0.050	0.05459
	CWI	-0.052 *	-0.149 ***	-0.120 ***	0.226 ***	0.094 **	0.03171
PH (cm)	FD	6.129 ***	7.486 ***	-7.086 ***	-1.621	-4.907 ***	0.81214
	CWI	0.707	5.350 ***	-7.614 ***	2.029 *	-0.471	0.94010
DH (no.)	FD	4.750 ***	-10.39 ***	-1.250 **	4.250 ***	2.643 ***	0.43087
	CWI	2.914 ***	-5.621 ***	-2.657 **	3.021 ***	2.343 **	0.79244
SER (cm/day)	FD	0.172 ***	0.400 ***	-0.204 ***	-0.159 ***	-0.210 ***	0.01434
	CWI	0.038 *	0.209 ***	-0.101 ***	-0.051***	-0.095 ***	0.01621
TLN (no./ 4 mp)	FD	-1.964 **	-4.538 ***	0.214	1.786 **	4.500 ***	0.61841
	CWI	-1.414 ***	-3.129 ***	-0.093	1.371 ***	3.264 ***	0.35930
GLN (no./ 4 mp)	FD	-1.057	-2.557 ***	-0.843	1.299 *	3.229 ***	0.54586
	CWI	-2.100 ***	-2.814 **	0.471	1.829 ***	2.614 ***	0.29172
Chl (%)	CWI	12.093 **	13.129 **	-4.800 **	-9.979 ***	-10.443 **	1.45502
AUCPC-value	CWI	192.05 **	259.30 **	-73.95 *	-204.20 **	-173.20 **	28.9230
SSI		0.033	0.070 ***	0.011	-0.058 **	-0.056 **	0.01771
STI		-0.021	-0.031**	-0.041 ***	0.052***	0.041 ***	0.01048

[+] See Table 3 for abbreviations; *,**,*** significantly different from 0 at 0.05, 0.01 and 0.001 levels of probability, respectively.

Specific combining ability (SCA) estimates:

The estimates of SCA effects in the 10 crosses for 18 characteristics studied in both FD- and CWI-experiments are presented in Table 6.6. The magnitude and property of SCA effects varied considerably between the two experiments, and among crosses and characteristics studied. In the FD-experiment, a cross between waterlogging-sensitive parents had positive SCA effects on 10 and negative SCA effects on four of the 14 characteristics studied; however, SCA effects were found significant only on GPSI, SER, TLN and DH. This cross exhibited the highest SCA value for TLN and the lowest SCA effect for BY. The three crosses between Et-13 and the waterlogging–tolerant parents had positive SCA effects on eight and negative SCA effects on four of the 14 characteristics; eight of them were significantly different from zero. One or more of these crosses contributed the lowest SCA effects for GYms, GPS, KM, GPSI, PH, DH and SER and the lowest SCA effects for TLN and PS. Crosses between K6290-Bulk and the tolerant parents exhibited SCA effects on GYts and TLN and positive SCA values on GYts, GYms, BY, KM, SIPS, PH and SER; only SCA effects on GYms, PH, SER and GLN were found significant in one or more of these crosses. The property of SCA effects on most of the characteristics were inconsistent across the three tolerant by tolerant crosses; nevertheless positive SCA effects on BY, PS, DH, TLN and negative SCA effects on GPSI and SER were consistently exhibited in all three crosses. The largest SCA effects on GYt was contributed by PRL/Sara x Ducula cross and the lowest was contributed by Vee/Myna x Ducula cross. The former cross also contributed the largest SCA effects for GYts, BY and TLN. Vee/Myna x Ducula and Vee/Myna x PRL/Sara crosses contributed the lowest SCA effects for GPSI and PS, respectively.

In the CWI-experiment, the cross between waterlogging-sensitive parents exhibited negative SCA effects for most characteristics except for five characteristics with positive SCA effects. Significant SCA effects, however, were detected only on BY, SER, TLN, GLN, Chl and AUCPC-value. This cross contributed the highest SCA effects for Chl and AUCPC-values and the lowest SCA effects for BY. The three ET-13 by tolerant parent crosses had SCA effects positive on eight and negative on seven of the 18 characteristics studied; those on 11 of these characteristics were significant in one or more of these crosses. The largest SCA effects for GPSI and SER were

contributed by ET-13 x Ducula crosses. The lowest SCA effects on GPS and PH were attributed to ET-13 x PRL/Sara cross and that on DH and TLN to ET-13 x Ducula cross. Positive SCA effects on eight and negative on three of the 18 characteristics were detected in all three crosses generated from K6290-Bulk by three tolerant parents; four of the characteristics with positive SCA effects and two with negative were observed in one or more of the crosses. The SCA effects for nine other characteristics varied with the direction across the crosses and five of the characteristics with positive and one with negative SCA values were significant in one or two of the three K6290-Bulk by tolerant crosses. The largest SCA effects on PH was attributed to K6290-Bulk x Vee/Myna crosses whereas those on BY and PS were attributed to K6290-Bulk x PRL/Sara crosses and that on GYms by K6290-Bulk x Ducula cross. This last cross also had the lowest SCA values for Chl and AUCPC-value, which are an important characteristics suggested as useful selection criteria in breeding for waterlogging tolerant genotypes (Van Ginkel *et al.*, 1992; Boru, 1996). The three tolerant by tolerant crosses had positive SCA effects on seven and negative on four of the 18 characteristics; SCA effects on five of these characteristics were significant at least in two of the three crosses. Of the remaining seven characteristics, four had positive and three had negative SCA effects in two of the three crosses. Vee/Myna x Ducula and PRL/Sara x Ducula crosses contributed the largest SCA effects on TLN and GPS. The former cross also had the lowest SCA value for GYt, GPSl and STI index. Veer/Myna x PRL/Sara cross also contributed the lowest SCA effects for GYts, PS and GLN.

Table 6.6. Specific combining ability of crosses for various characteristics of wheat in the free drainage and waterlogging greenhouse experiments in 1999/2000

Character[+]	Exper-iment	Crosses										SEsca
		ET x Bulk	ET x Vee	Et x PRL	Et x Duc.	Bulk x Vee	Bulk x PRL	Bulk x Duc	Veex PRL	Vee x Duc.	PRL x Duc	
GYt (g/pot)	FD	0.830	1.180	2.619	1.994	0.376	0.362	0.687	1.315	-4.635**	3.801*	1.47728
	WL	-0.932	2.568***	1.700**	1.950 **	0.204	1.936**	0.986	-1.339*	-1.839**	-0.232	0.62078
GYms (g/pot)	FD	0.763	2.106***	2.606***	2.056***	0.860	0.635	1.360*	0.127	-0.998	-0.573	0.50981
	WL	-0.476	0.238	0.235	0.306	0.938*	0.435	1.156**	0.849	-0.480	0.242	0.36059
GYts (g/pot	FD	0.051	-0.935	0.001	-0.070	-0.485	-0.274	-0.645	1.190*	-3.631***	4.380***	0.50981
	WL	-0.456	2.298***	1.451*	1.598*	-0.738	1.515*	-0.138	-2.181**	-1.360*	-0.481	0.63954
BY (g/pot)	FD	-3.788	-6.145	-2.824	-4.681	1.698	1.894	1.437	2.087	-3.820	11.226*	3.17581
	WL	-4.276*	4.242*	0.513	1.431	-0.730	4.667*	0.835	-0.115	1.177	3.174	1.94737
GPS (no.)	FD	1.790	0.551	6.251	7.248*	5.212	-5.113	3.858	-4.002	-9.106*	1.119	3.39073
	WL	-1.332	-0.343	-4.143*	-1.868	1.057	-3.348	-3.718*	0.096	2.046	4.496*	1.79263
KM (mg/ grain)	FD	0.580	3.912*	3.387	0.476	1.344	2.669	2.483	3.626*	2.767	-0.766	1.71101
	WL	-0.810	6.369***	5.376**	2.048	2.876	6.133***	4.505**	2.712	1.433	1.541	1.64577
PS (no./pot)	FD	-0.786	-0.821	-1.964*	-1.943*	-0.964	0.393	-0.786	0.107	0.179	1.036	0.82552
	WL	-0.869	2.095*	2.310**	2.060*	-0.226	2.738***	1.738*	-3.048***	-2.798***	-1.833*	0.78699
SIPS (no.)	FD	-1.940	0.167	3.060	2.667	3.202	0.845	1.702	0.202	0.310	-3.298	2.49928
	WL	-5.214	-0.643	-1.464	-4.321	3.821	3.000	4.893	2.571	1.964	-3.107	2.56878
GPSI (no.)	FD	0.253*	0.321*	0.407**	0.366*	-0.019	-0.234	0.127	-0.233	-0.330*	-0.0003	0.14094
	WL	-0.006	-0.035	0.044	0.301**	0.137	-0.110	-0.002	-0.063	-0.206*	0.098	0.08186
PH (cm)	FD	1.619	0.190	9.226***	5.512*	6.833**	0.369	5.655*	-2.810	-1.524	0.762	2.09693
	WL	0.310	2.024	-2.869	0.131	4.881	4.738	2.238	2.202	0.202	1.310	2.42733
DH (no.)	FD	-10.94***	-15.33***	13.58***	-14.98***	3.060**	-3.94**	0.420	1.67	7.77***	2.52*	1.11249
	WL	-0.729	-7.940***	-3.119	-9.190***	0.345	-3.583	-2.655	0.452	2.881	2.202	2.04607
SER (cm/day)	FD	0.208 ***	0.331***	0.205***	0.271***	0.058	0.086*	0.116**	-0.043	-0.093*	-0.062	0.03702
	WL	0.097 *	0.145**	0.165***	0.175***	0.048	-0.010	0.011	-0.022	-0.022	-0.038	0.04184
TLN (no./ 4 MP)	FD	3.333 *	-4.167*	-3.738*	-4.452**	-0.595	-2.167	-2.881	2.083	1.369	0.798	1.59672
	WL	-1.940*	-2.976**	-1.440*	-4.333***	-1.262	0.274	0.381	0.238	2.595**	-0.619	0.92770
GLN (no./ 4 MP)	FD	3.048	-1.667	-2.238	-2.238	0.333	-2.738	-0.738	1.548	0.548	-0.524	1.40940
	WL	-1.702*	0.512	-0.095	-0.881	-0.024	1.119	1.583*	-2.917**	-0.452	0.440	0.75322
Chl (%)	WL	10.51 **	-16.56***	-11.88**	-7.67*	-10.10*	-8.67*	-18.20***	8.76*	9.73*	3.90	3.75684
AUCPC-value	WL	169.4 *	-153.6*	-229.9**	-117.4	-243.6**	-165.9*	-249.4**	135.9	82.1	37.4	74.6789
SSI		0.053	-0.112	-0.037	-0.067	0.001	-0.079	-0.030	0.104	0.002	0.069	0.04573
STI		-0.028	0.093**	0.086**	0.085**	0.013	0.073*	0.042	-0.030	-0.111***	0.047	0.02707

[+] See Table 3 for abbreviations; *,**,*** significantly different from 0 at 0.05, 0.01 and 0.001 levels of probability, respectively.

Estimates of genetic parameters:

Estimates of variance for combining ability and genetic parameters are given in Table 6.7. The results indicated that genotypic variability accounted for most of the total variability for characteristics studied. Relatively large estimates of V_D observed for some of the characteristics also indicated that there was non-additivity for some genes controlling these characteristics, as shown by high SCA effects for some of the crosses in Table 6.6. Estimates of V_A for GYts in both experiments, GYT and GPS in FD- and PS in the CWl-experiment as well as estimates of V_D for SlPS in the CWl- experiment, however, were negative and the values were less than the values of their corresponding error variance, suggesting that the true value of the variances is either zero or a value close to zero. The most likely explanation under such circumstance appears to be low magnitude of V_A in relation to V_E rather than non-existence of genetic variation (i.e., V_A being zero) and hence, low rather than null heritability of characteristics.

In both experimental conditions, the relative proportion of V_A estimates to that of V_D varied considerably across the characteristics studied. Heritability and PR ratio estimates were also variable between the two experimental conditions and among characteristics studied. In the FD-experiment, V_A was relatively more important than V_D for GPS, PS, SlPS, PH, SER, TLN and GLN. This was supported by high value of both h^2_b and h^2_n heritabilities and high PR ratios; whereas for GYt, GYms, GYts, BY, KM, GPSl and HD characteristics, V_D estimates were relatively larger than V_A estimates. The h^2_n and PR ratios of these characteristics were very low although h^2_b estimates remain fairly high. In CWl-experiment, the magnitude of V_A was larger than V_D for GYms, BY, GPS, SlPS, GPSl, PH and SER, which was supported by fairly large heritability estimates (h^2_b and h^2_n) and PR ratios. Relatively larger V_D estimates than V_A were recorded for GYt, GYts, KM, PS and HD, which was also implicated by low estimates of h^2_n and PR ratios. In general, h^2_b estimates for most characteristics have been higher than h^2_n estimates, substantiating the evidence that non-additive gene effects also add to the total genetic variance. The waterlogging tolerance as measured by TLN, GLN, Chl and AUCPC-value was mainly controlled by additive genes, as the estimates for V_A were relatively larger than for V_D estimates. This was supported by relatively high estimates of both h^2_b and h^2_n and PR ratios, which ranges between 93.0 to 95.3%, 57.3

to 83.9% and 0.602 to 0.890 units, respectively. Relatively large estimates of GCA/SCA mean square ratios for most of these characteristics in Table 6.3 also present additional evidence that V_A was relatively more important than V_D in the inheritance of characteristics related to tolerance to the waterlogging stress. These results are in agreement with the findings of Boru (1996) who reported the relatively greater importance of V_A component than V_D for waterlogging tolerance of wheat in the extended field experiments in Mexico. He also reported high h^2_b estimates for Chl and AUCPC-value. The two yield based indices (SSI and STI) had larger V_A estimates than V_D estimates; The SSI and STI indices had 73.1 and 95.7 % h^2_b, 48.0 and 69.0% h^2_b and 0.66 and 0.72 units of PR ratios. Hence, inheritance of yield-based indices was mainly governed by additive gene action like other characteristics relevant to waterlogging tolerance.

The average degree of dominance was estimated by $\sqrt{H/D}$ (Singh and Chaudhary, 1979). If there were complete dominance at every locus, the value of $\sqrt{H/D}$ would be 1; with partial dominance, between 0 and 1; and with over dominance, greater than 1. In the FD-experiment, there were indications of over-dominance for four and partial dominance for two of the characteristics studied; the values of dominance ratio for PS, PH, SER and TLN were close to complete dominance. In the CWl-experiment, the estimates of dominance ratios were in the range of over-dominance for four of the characteristics and in the partial dominance range for six others. The ratios for the remaining four characteristics were close to complete dominance. The dominance ratios for characteristics related to waterlogging tolerance were close to complete dominance except for GLN for which the value was within the range of partial dominance. The degree of dominance for both SSI and STI indices (0.722 and 0.880 units, respectively) were close to complete dominance. These results suggested that waterlogging tolerance in wheat was within the range of partial and complete dominance. Submergence tolerance in rice and pre-emergence flooding tolerance in sorghum were also reported to be within the range of partial and complete dominance (Haque *et al.*, 1989) and partial dominance (Thseng and Hou, 1993), respectively.

Table 6.7. Estimates of combining ability variance and genetic parameters for various wheat characteristics in the free drainage and waterlogging greenhouse pot experiments in 1999/2000

Character*	Exper-iment	$\delta^2 gca$	$\delta^2 sca$	$V_A = 2\delta^2 gca$	$V_D = \delta^2 sca$	$V_G = V_A + V_D$	V_E	$V_P = V_G + V_E$	h^2_b	h^2_n	PR	$\sqrt{H/D}$
Gyt (g/pot)	FD	-0.407	5.295	-0.814	5.295	5.295	2.864	8.159	0.649	0	0.	0
	CWI	0.795	2.857	1.590	2.857	4.447	0.506	4.952	0.899	0.321	0.358	1.896
Gyms (g/pot)	FD	0.035	3.830	0.071	3.830	3.901	0.341	4.240	0.920	0.017	0.018	10.461
	CWI	0.946	0.496	1.893	0.496	2.389	0.171	2.560	0.933	0.740	0.792	0.724
Gyts (g/pot	FD	-0.524	2.438	-1.048	2.438	2.438	2.244	4.682	0.521	0	0	0
	CWI	-0.220	2.150	-0.440	2.150	2.150	0.537	2.687	0.800	0	0	0
BY (g/pot)	FD	3.617	23.176	7.235	23.176	30.411	13.238	43.648	0.697	0.166	0.238	2.531
	CWI	3.199	5.741	6.398	5.741	12.139	4.977	17.116	0.709	0.374	0.527	1.340
GPS (no.)	FD	43.990	20.027	87.980	20.027	108.007	15.090	123.097	8.877	0.715	0.815	0.675
	CWI	14.694	6.348	29.388	6.348	35.736	4.218	39.954	0.894	0.736	0.822	0.657
KM (mg/grain)	FD	5.213	11.66	10.426	11.66	22.089	3.842	25.932	0.852	0.402	0.472	1.496
	CWI	10.382	32.885	20.765	32.885	53.649	3.555	57.204	0.938	0.363	0.387	1.780
PS (no./pot)	FD	1.471	1.064	2.941	1.064	4.005	0.894	4.900	0.817	0.600	0.734	0.602
	CWI	-0.224	5.245	-0.447	5.245	5.245	0.813	6.058	0.866	0	0	0
SlPS (no.)	FD	23.440	-2.490	46.880	-2.490	46.880	8.198	55.078	0.851	0.850	1.065	0
	CWI	19.879	8.914	39.757	8.914	48.671	8.661	57.332	0.849	0.694	0.817	0.670
GPS (no.)	FD	-0.006	0.092	-0.011	0.092	0.081	0.026	0.107	0.756	0	0	0
	CWI	0.023	0.013	0.043	0.013	0.057	0.009	0.065	0.866	0.663	0.767	0.781
PH (cm)	FD	37.318	31.401	74.635	31.401	106.037	5.771	111.808	0.948	0.668	0.704	0.917
	CWI	20.859	6.272	41.717	6.272	47.989	7.733	55.722	0.861	0.749	0.869	0.548
HD (no.)	FD	15.104	167.72	30.208	167.718	197.926	1.624	199.551	0.992	0.151	0.153	3.332
	CWI	10.698	27.721	21.396	27.721	49.117	5.495	54.611	0.899	0.392	0.436	1.610
SER (cm/day)	FD	0.066	0.064	0.132	0.064	0.196	0.002	0.198	0.990	0.667	0.667	1.016
	CWI	0.014	0.017	0.028	0.017	0.045	0.002	0.047	0.951	0.589	0.619	1.102
TLN (no./4 MP)	FD	10.357	8.009	20.714	8.009	28.722	3.346	32.068	0.896	0.646	0.721	0.880
	CWI	5.016	6.343	10.032	6.343	16.375	1.130	17.504	0.936	0.573	0.613	1.125
GLN (no./ 4 MP)	FD	4.342	2.526	8.683	2.526	11.210	2.607	13.817	0.811	0.628	0.775	0.763
	CWI	5.386	1.330	10.773	1.330	12.102	0.745	12.847	0.942	0.839	0.890	0.497
Chl (%)	CWI	113.45	150.27	226.90	150.27	377.18	18.524	395.701	0.953	0.573	0.602	1.151
AUCPC-Value	CWI	39355	34445	78709	34445	113153	7319.7	120473	0.939	0.653	0.696	0.936
SSI		0.0024	0.0025	0.0048	0.0025	0.0073	0.0027	0.010	0.731	0.480	0.658	0.722
STI		0.008	0.0062	0.016	0.0062	0.0222	0.0010	0.0232	0.957	0.690	0.721	0.880

See Table 3 for abbreviations; δ^2_{gca},δ^2_{sca}, represent variance due to gca and sca; V_A, V_D, V_G, V_P and V_E additive, dominance, genotypic, phenotypic and error variance, respectively; PR=predictability ratio; $\sqrt{H/D}$=Degree of average dominance; zero denotes negative h^2_n and PR values.

Heterosis estimates:

Mean squares of characteristics from separate analysis of variance for parents and F_1 hybrids are presented in Table 6.8. The analysis indicated that there were significant differences among parents for all characteristics measured in both experiments except GYt and GYts in the FD- and GYts and BY in the CWI-experiments. F_1 hybrids also exhibited significant differences for all measured characteristics except for GYts and PS in the FD-experiment and for SSI index. Average performance of F_1 hybrids was higher than parents for GYt, GYms, KM, SIPS and GPSI in both experiments and GPS in FD- and GYts, BY and PS in the CWI-experiments. Compared to parents, F_1 hybrids produced taller plants, were earlier to head, had fewer TLN and GLN, and exhibited lower Chl and AUCPC-value. F_1 hybrids also showed lower values of SSI index and greater STI index than the parents. The significance of parent vs F_1 hybrid mean square contrasts in Table 6.3 also showed the existence of heterosis for most measured characteristics in both experiments.

The mean percent mid- and high-parent heterosis detected in the 10 hybrids for characteristics measured in both FD- and CWI-experiments are given in Tables 6.9 and 6.10, respectively. In both experiments, significant heterosis was observed in both directions for all characteristics in certain hybrid combinations. The degree of expression of the heterosis at the two experimental conditions varies considerably for the different characteristics. Some crosses were markedly heterotic (either positively or negatively), whereas others showed only modest or negligible responses. Differential expression of heterosis in wheat under varying stress conditions has been reported in a number of studies (Sinolinding and Chowdhry, 1974; Rehman, 1978; Pattak and Nema, 1988). Heterosis estimates in this study were generally higher for GYt, GYts, BY, KM and PS in the CWI-experiment, for GYms, GPS, GPSI, PH, DH and SER in the FD-experiment, and comparable for SIPS, TLN and GLN in both experiments. In both experiments, the maximum mid-parent heterosis was expressed by SER followed by GYms, GYts and HD in the FD-experiment and by KM, Chl and GYms in the CWI-experiment. The average mid-parent heterosis of 9.1 and 15.5% for GYt, 26.0 and 20.0% for GYms, -0.1 and 12.5% for GYts, and -0.7 and 5.1% for BY were recorded in the CWI- and FD-experiments, respectively. The corresponding figures for GPS, KM

and PS were –8.4, 25.9 and 7.8% in the FD- and 6.17, 12.9 and –10.8% in the CWI-experiments. These results generally indicate a better expression of heterosis under waterlogging than under free drainage condition. Studies with wheat (Grant and McKenzie, 1970; Jordaan, 1999), rice (Young and Virmani, 1990), sorghum (Haussman *et al.*, 1988) and pearl millet (Yadav *et al.*, 2000) also showed that heterosis contributed to yield superiority as much or more in stress environments than in more favourable environments.

In the FD-experiment, PRL/Sara x Ducula exhibited the highest positive mid- or both mid- and high-parent heterosis for GYt, GYts and BY. Significantly high positive heterosis for GYt was also detected in the Et-13 x PRL/Sara cross. Et-13 x PRL/Sara and PRL/Sara x Ducula crosses maintained their heterotic significance for GYt and BY, respectively, under waterlogging stress conditions. In addition, ET-13 x Vee/Myna for both GYt and BY and ET-13 x Ducula for GYt showed significant mid-parent heterosis in the CWI-experiment. Significantly high negative heterosis for GYt and GYts in both experiments, and for GPS in the FD-experiment were revealed by Vee/Myna x Ducula cross; the latter character had negative heterosis in CWI-experiment except for mid-parent heterosis for tolerant x tolerant crosses. Vee/Myna was implicated in Table 6.5 as a poor general combiner for these characteristics. Significantly large mid- or both mid- and high-parent heterosis were recorded in the FD-experiment when ET-13 or K6290-Bulk was used as one of the parents, and in the CWI-experiment when ET-13 used as one of the parents. Crosses involving ET-13 as parent had the highest negative heterosis for BY and positive heterosis for GPSI in the FD- experiment; however, only ET-13 x K6290-Bulk and ET-13 x Ducula maintained such trend under waterlogging stress conditions.

Table 6.8. Mean squares and means of parents and F_1 hybrids, and percent heterosis for various characteristics of wheat genotypes in the free drainage and waterlogging greenhouse pot experiments in 1999/2000

Character+	Experiment	Mean square		Mean	
		Parent (4)	F_1 hybrid (9)	Parent	F_1 hybrid
Gyt(g/pot)	FD	11.523ns	30.875*	28.679	31.230
	CWI	28.272***	14.916***	9.940	11.440
GYms (g/pot)	FD	21.446***	6.203**	10.975	13.658
	CWI	15.589***	7.419**	5.300	6.327
GYts (g/pot	FD	14.279ns	16.242ns	17.700	17.575
	CWI	2.372ns	12.626***	4.660	5.113
BYM (g/pot)	FD	315.46***	130.250*	67.53	66.655
	CWI	33.756ns	75.608**	31.060	34.335
GPS (no.)	FD	954.12***	333.75**	46.850	49.193
	CWI	240.80***	134.951***	25.080	22.965
KM(mg/grain)	FD	117.59**	51.914*	48.285	54.497
	CWI	284.56***	91.366***	36.095	45.750
PS (no./pot)	FD	49.425***	4.847ns	13.700	12.125
	CWI	16.30*	27.04***	10.550	11.200
SIPS (no.)	FD	445.45***	122.86**	80.150	82.225
	CWI	373.33**	190.511***	59.900	60.35
GPSI (no.)	FD	0.708*	0.294**	2.790	2.988
	CWI	0.408***	0.223***	2.100	2.147
PHm (cm)	FD	457.70***	403.289***	107.850	115.600
	CWI	383.45**	145.622***	94.100	98.650
DH (no.)	FD	1501.0***	324.167***	82.500	69.50
	CWI	378.43**	110.933**	85.200	78.800
SERcm/day)	FD	0.856***	0.693***	0.831	1.155
	CWI	0.268***	0.135***	0.610	0.774
TLN (no./ 4MP)	FD	202.50***	95.069***	47.000	43.875
	CWI	83.80***	60.667***	45.300	42.575
GLN (no./ 4MP)	FD	110.80***	32.444*	24.200	22.500
	CWI	94.70***	37.069***	12.100	11.375
Chl (%)	CWI	3109***	865.222***	44.80	32.750
AUCPC-VALUE	CWI	918316***	269440***	1060.150	839.650
SSI		0.079**	0.026ns	1.013	0.984
STI		0.031***	0.032***	0.309	0.390

+ See Table 3 for abbreviations; Numbers in parenthesis represent degrees of freedom; *,**,*** significant at the probability levels of 5, 1 and 0.1%, respectively.

All crosses showed significantly positive mid- or both mid- and high-parent heterosis for KM in the CWl-experiment; however, only five of the 10 crosses exhibited significant heterosis for KM in the FD-experiment. Most crosses involving ET-13 as parent had significant mid-parent heterosis for PS in both experiments but opposite in direction. None of the crosses showed heterosis for SlPS in both experiments except Vee/Myna x PRL/Sara and Vee/Myna x Ducula in the FD-experiment and three of the four crosses included Et-13 as parent in the CWl-experiment.

In both experiments, there were significant heterosis for tallness and earliness. Most crosses included either ET-13, K6290-Bulk, or both revealed the largest significant heterosis for earliness. These crosses in the FD-experiment exhibited the largest significant heterosis for tallness. Both Et-13 and K6290-Bulk were good general combiners for PH and K6290-Bulk for DH (Table 6.4). In both experiments, all crosses expressed positive heterosis for SER; the largest heterosis for SER was observed in crosses which included ET-13 or K6290-Bulk as one of the parents. Significantly large negative heterosis for TLN and GLN in both experiments expressed by most crosses involved Et-13 or K6290-Bulk as parents. The largest significant negative mid-parent heterosis for Chl and AUCPC-value were evident when ET-13 and K6290-Bulk were crossed with tolerant genotypes (Table 6.10).

Table 6.9. Estimates of mid-parent and high-parent heterosis for various characteristics of wheat in the free drainage greenhouse pot-experiment in 1999/2000

Crosses	Et x Bulk		ET x Vee		ET x PRL		Et x Duc.		Bulk x Vee		Bulk x PRL		Bulk x Duc.		Vee x PRL		Vee x Duc.		PRL x Duc.		Average	
Character[+]	MPH	HPH	MPH	HPH	MPH	HPH	MPH	HPH	MPH	HPH	MPH	HPH	MPH	HPH	MPH	HPH	MPH	HPH	MPH	HPH	MPH	HPH
GYt (g/pot)	10.62	2.95	8.66	4.51	23.14 **	19.99 *	14.56	7.85	1.79	-1.65	10.01	4.94	5.70	4.41	10.23	8.77	-15.83 *	-17.70 *	21.71 **	17.47 *	9.06	5.15
GYms (g/pot)	37.13 ***	12.54	51.71 ***	32.87 ***	49.91 ***	17.08 **	43.92 ***	15.00 *	21.43 *	12.52	17.77 **	10.49	22.43 ***	18.30 **	11.64	-2.44	-0.20	-10.40	4.55	1.39	26.03	10.74
GYts (g/pot)	-2.76	-2.95	-11.32	-11.99	6.51	-5.89	-1.58	-5.52	-9.50	-10.36	4.23	-8.05	-5.41	-9.37	9.24	-2.82	-25.57 *	-28.02 *	35.58 **	24.34 *	10.06	-6.06
BY (g/pot)	-10.61	-20.66 ***	-16.66 **	-27.59 ***	-5.59	-16.91 **	-10.75	-20.39 **	0.72	-1.73	8.31	7.25	4.30	3.73	5.89	4.33	-6.78	-9.53	23.95 **	22.06 **	-0.72	-5.95
GPS (no.)	19.49	5.66	7.49	-2.27	18.76 *	-14.25	29.75 *	7.80	11.84	8.44	-7.22	-26.80 **	13.46	5.58	-11.18	-31.49 ***	-23.12 *	-30.48 ***	2.44	-14.41	6.17	-9.22
KM (mg/grain)	9.21	-1.36	18.66 ***	8.01	18.28 **	16.52 *	8.24	0.37	11.31 *	10.35 *	14.10 **	1.69	10.63 *	7.51	18.74 ***	6.64	13.52 **	11.27 *	6.62	-2.49	12.93	5.83
PS (no./pot)	-16.03 *	-27.37 ***	-15.15 *	-26.32 ***	-23.67 **	-43.16 ***	-20.63 **	-34.21 ***	-13.67	-14.29	-2.16	-18.12	-12.55	-16.67	-3.00	-19.29 *	-3.40	-8.57	5.51	-8.00	-10.48	-21.60
SIPS (no.)	0	-0.65	2.94	-3.29	5.06	-5.00	4.91	1.72	7.09	0	2.34	-6.91	3.66	-2.30	1.74	-12.98 **	2.08	-9.77 *	-2.98	-6.60	2.68	-4.58
GPSI (no.)	25.02 **	10.58	23.33 **	7.27	26.60 ***	4.36	30.35 ***	16.49	-1.85	-3.74	-7.09	-14.37 *	7.16	5.97	-10.01	-15.54 *	-12.53	-15.18	0.86	-8.03	8.18	-1.22
PH (cm)	7.91 **	6.21	4.71	-4.02	13.72 ***	8.38 **	11.44 ***	2.39	10.22 ***	-0.41	5.20	-1.24	10.88 ***	0.41	-0.25	-4.25	1.79	1.53	5.20	1.23	7.08	1.02
DH (days)	-40.93 ***	-48.29 ***	-32.46 ***	-44.04 ***	-30.63 ***	-37.45 ***	-30.97 ***	-40.16 ***	-0.76	-10.30 ***	-13.67 ***	-28.31 ***	-5.07 *	-18.20 ***	-2.97	-11.80 ***	7.72 ***	2.09	-2.17	-6.40 **	-15.19	-24.29
SER (cm/day)	46.42 ***	13.25 ***	93.19 ***	52.70 ***	66.54 ***	43.29 ***	83.63 ***	45.07 ***	22.43 ***	-19.34 ***	22.11 ***	-14.87 ***	27.32 ***	-16.15 ***	11.69	0.85	5.47	5.40	7.41	-3.08	38.62	10.71
TLN (no./ 4 MP)	1.33	-8.13	-14.75 **	-15.22 **	-14.14 **	-18.00 **	-15.69 ***	-23.89 ***	-3.61	-13.04 *	-8.05	-20.00 ***	-10.16 *	-25.66 ***	2.08	-2.00	-0.49	-9.73 *	-2.35	-7.96	-6.58	-14.36
GLN (no./4MP)	9.76	-2.17	-11.36	-7.14	-21.57 **	-28.57 ***	-14.81 *	-25.81 ***	2.56	-4.76	-17.39 *	-32.14 ***	-6.12	-25.81 ***	2.04	-10.71	0	-16.13 *	-8.47	-12.90	-6.54	-16.61

[+] See Table 3 for abbreviations; MPH=mid-parent heterosis; HPH=high-parent heterosis;*,**,*** significantly different from zero at 0.05, 0.01 and 0.001 levels of probability, respectively.

Table 6.10. Estimates of mid- and high-parent heterosis for various wheat characteristics in the waterlogging greenhouse pot-experiment in 1999/2000

Crosses	Et x Bulk		ET x Vee		ET x PRL		Et x Duc.		Bulk x Vee		Bulk x PRL		Bulk x Duc.		Vee x PRL		Vee x Duc.		PRL x Duc.		Average	
Charcter[+]	MPH	HPH	MPH	HPH	MPH	HPH	MPH	HPH	MPH	HPH	MPH	HPH	MPH	HPH	MPH	HPH	MPH	HPH	MPH	HPH	MPH	HPH
GYt (g/pot)	12.93	8.48	45.24 ***	25.72 *	26.27 ***	6.59	35.30 ***	5.13	7.58	-3.52	29.74 ***	4.62	17.35	-6.04	-8.13	-18.61 *	-15.35	-25.60 ***	4.20	3.14	15.51	-0.01
GYms (g/pot)	2.93	-1.20	17.28	3.89	13.76	-13.71	12.40	-16.84 *	45.60 ***	23.61	26.20 **	-7.39	35.71 ***	-2.71	28.36 **	7.19	3.65	-15.96 *	13.59	9.48	19.95	-1.36
GYts (g/pot)	20.77	8.57	72.02 ***	46.84 *	62.33 ***	33.12	64.32 ***	38.02	-25.57	-29.20	33.54	20.33	-3.91	-11.02	-50.23 ***	-52.59 ***	-38.85 *	-40.04	-9.20	-11.85	12.52	0.22
BY (g/pot)	-12.84	-16.22	19.62 *	19.46	9.68	4.89	11.00	2.89	1.86	-1.97	22.63 *	12.94	8.28	-3.21	9.84	4.92	12.23	3.91	20.23 *	16.36	5.06	4.40
GPS (no.)	-22.95 *	-28.13 *	-7.96	-23.95 *	-23.32 **	-35.18 ***	-12.94	-23.61 *	-0.32	-12.60	-21.59 *	-37.36 ***	-20.51 *	-34.29 ***	0.45	-27.14 ***	12.74	-15.87	12.21	7.45	-8.42	-23.07
KM (mg/grain)	19.71 *	12.29	38.03 ***	13.08 *	41.31 ***	25.51 ***	20.74 ***	-5.71	26.02 ***	8.93	40.92 ***	32.90 ***	25.89 ***	3.31	26.43 ***	15.24 *	13.52 ***	11.27	6.62 ***	-2.49	25.92	11.43
PS(no./pot)	13.99	10.00	20.83 *	3.57	36.59 ***	33.33 **	34.74 ***	28.00 *	-3.00	-19.29 *	36.36 ***	28.57 *	25.68 *	23.66	-32.25 ***	-40.71 ***	-34.78 ***	-84.18 ***	-20.00	-25.71 *	7.82	-4.28
SIPS (no.)	-12.12	-15.63 *	-3.08	-7.64	-6.47	-15.89 ***	-11.64 *	-20.29 ***	14.40 *	13.51	7.93	-6.38	10.51	-3.86	7.82	-7.09	6.28	-8.14	-4.20	-4.54	0.94	-7.60
GPSI (no.)	3.17	0.68	0.36	-1.37	4.02	-9.99	20.01 ***	12.10	6.06	1.77	-5.06	-19.52 ***	3.74	-5.92	-4.53	-16.15	-9.29	-13.87	5.82	-2.56	2.05	-5.48
PH (cm)	3.90	1.67	4.83	-6.58	-1.67	-1.82	0.98	-1.32	11.45 ***	-1.97	9.14 *	7.37	6.37	2.46	6.71	-4.77	4.08	-5.30	3.73	1.52	4.95	-0.87
DH (days)	-8.98 *	-20.35 ***	-16.28 ***	-24.67 ***	-10.04 ***	-13.88 ***	-17.34 ***	-20.86 ***	-3.18	-6.17	-7.65 *	-15.96 ***	-7.41 *	-15.73 ***	-1.92	-8.09 *	0.12	-6.18	-0.56	-0.56	-7.32	-10.47
SER (cm/day	35.47 ***	-0.18	69.25 ***	58.99 ***	62.12 ***	52.86 ***	72.40 ***	66.07 ***	16.05 *	-17.82 ***	6.02	-18.64 ***	10.20	-20.72 ***	7.57	-4.35	10.31	7.47	3.25	-6.01 *	29.26	11.77
TLN (no./ 4 MP)	-12.43 ***	-19.56 ***	-13.33 ***	-15.22 ***	-9.68 ***	-10.64 ***	-15.46 ***	-19.61 ***	-5.46	-11.36 ***	-1.75	-10.64 ***	-1.68	-13.73 ***	-1.10	-4.26	3.79	-3.33	-3.06	-6.86	-6.02	-11.52
GLN (no./4MP	-28.57 *	-41.18 ***	-6.67	-25.00 ***	-7.76	-29.38 ***	-9.60	-31.52 ***	-4.62	-33.93 ***	9.77	-26.25 ***	18.18	-21.21 ***	-26.67 ***	-31.25 ***	-6.23	-13.33	1.54	0	-6.11	-25.31
Chl (%)	-3.40	-1.70	-47.69 ***	-12.00	-42.92 ***	-30.12	-35.70 ***	-39.77	-34.94 ***	-12.00	-35.53 ***	-50.60	-56.66 ***	-34.09	18.23	45.78	17.46	42.05	-5.14	-2.41	-22.63	23.72
AUCPC-Value	-2.29	-4.84	-24.27 *	-2.66	-35.44 *	-9.03	-24.34 ***	-17.99	-32.46 ***	0	-30.00 ***	-30.26	-36.64 ***	-8.62	4.82	-25.14	-3.17	-8.37	-5.14	-6.96	-18.89	9.99

[+] See Table 3 for abbreviations; MPH=mid-parent heterosis; HPH=high-parent heterosis;*,**,*** significantly different from zero at 0.05, 0.01 and 0.001 levels of probability, respectively.

Association of parental divergence with F_1 performance and SCA effects:

The magnitude of heterotic responses of F_1 hybrids and SCA effects are considered to be related to the degree of genetic divergence among the parents involved in the crosses (Gallais, 1988). In this study, genetic divergence of parental genotypes was assessed based on pedigree information (1-r) and seed storage protein markers (GD-SSP) (Table 6.2). Genetic distance based upon pedigree (1-r) between pairs of parental lines varied from 0.648 for cross Ducula x PRL/Sara to 0.988 for crosses PRL/Sara x K6290-Bulk and Ducula x K6290-Bulk with an average of 0.909 units. Similarly, the genetic distances based upon GD-SSP varied from 0.614 for K6290-Bulk x Ducula to 0.711 for PRL/Sara x Ducula with an average of 0.641 units. The mean distance from 1-r was 41% higher than that for GD-SSP distance. The rank correlation between 1-r and GD-SSP distances was –0.665*, indicating that these two genetic distance measures provide different results in estimating F_1 hybrid performance and SCA effects.

Spearman rank correlation of 1-r and GD-SSP with F_1 hybrid performance and SCA effects for various characteristics measured in both experiments are presented in Table 6.11. In both experiments, correlation of 1-r and GD-SSP with F_1 performance and SCA effects of crosses were weak and insignificant for most of the characteristics studied. However, significant correlations (positive or negative) between 1-r or GD-SSP and F_1 performance was observed on PH, DH, SER, TLN and GLN in the FD-experiment and on BY, GPS, PH, DH and SER in the CWl-experiment. Significant rank correlations between SCA effects and 1-r distances were detected on SlPS in the FD-experiment and on GPS, PS and AUCPC-value in CWl-experiment, whereas significant correlations between SCA effects and GD-SSP distances were detected only on GYms and PH in the FD- and on GPS and AUCPC-value in the CWl-experiments.

Table 6.11. Rank correlations of two genetic diversity measures of parents with F_1 performance and SCA effects of characteristics of wheat genotypes grown in the free drainage and waterlogging greenhouse pot experiments in 1999/2000

Characteristic	Free drainage experiment				Continuous waterlogging experiment			
	F_1 performance		SCA		F_1 performance		SCA	
	1-r	GD-SSP	1-r	GD-SSP	1-r	GD-SSP	1-r	GD-SSP
Gyt(g/pot)	0.043	-0.037	-0.482	0.165	-0.134	0.214	0.390	-0.153
GYms (g/pot)	0.445	-0.447	0.378	-0.557†	-0.287	0.385	-0.470	0.208
GYts (g/pot	-0.213	0.141	-0.299	0.104	0.091	-0.073	0.134	-0.749
BY (g/pot)	0.183	-0.110	-0.055	0.006	-0.437	0.727*	-0.104	0.495
GPS (no.)	0.092	-0.153	0.305	-0.385	-0.701*	0.667*	-0.646*	0.710*
KM(mg/grain)	0.287	-0.171	-0.146	-0.245	-0.341	0.428	0.354	-0.398
PS (no./pot)	-0.081	0.323	-0.266	0.500	0.457	-0.459	0.573†	-0.428
SIPS (no.)	-0.049	-0.006	0.531†	-0.508	0.162	-0.129	0.427	-0.336
GPSI (no.)	0.034	-0.196	0.067	-0.312	-0.177	0.184	-0.073	0.092
PH (cm)	0.665*	-0.789**	0.512	-0.630*	0.695*	-0.343	0.463	-0.177
DH (no.)	-0.640*	0.404	-0.201	0.208	-0.679*	0.281	-0.494	0.251
SERcm/day)	0.817**	-0.557†	0.378	-0.330	0.744*	-0.789**	0.372	-0.398
TLN (no./ 4MP)	-0.590†	0.574†	-0.250	0.092	-0.506	0.418	0.031	-0.006
GLN (no./4MP)	-0.628*	0.560†	-0.274	0.196	-0.269	0.408	0.421	-0.202
Chl (%)	------	-------	------	-------	0.334	-0.114	-0.305	0.434
AUCPC-VALUE	-------	--------	-------	-------	0.433	-0.165	-0.591†	0.545†

[+] See Table 3 for abbreviations; Numbers in parenthesis represent degrees of freedom; †,*,**,*** significant at the probability levels of 10, 5, 1 and 0.1%, respectively.

Associations among characteristics:

In order to understand the nature and degree of interrelationships among the different characteristics, both genotypic (r_g) and phenotypic (r_p) correlations were computed for all possible pairs of characteristics in both experiments (Tables 6.12 and 6.13). For most characteristics in both experiments, the magnitudes of r_g coefficients were generally larger than those of r_p. In both experiments, GYt was correlated positively genotypically and phenotypically with GYms, GYst and with all components of yield except with PS where both correlations were negative in FD-experiment; both r_g and r_p correlations of GYt with KM and r_p correlation with PS were weak and insignificant in the FD-experiment. Although both r_g and r_p correlations between GYt and BY were near zero in the FD-experiment, their correlations in the CWl-

experiment (r_g = 0.823*** and r_p = 0.707***) were significant and positive. In the CWI-experiment, the characteristics PH, DH and SER exerted no significant r_g or r_p influence on GYT, whereas in the FD-experiment, both r_g and r_p of PH (positive) and DH (negative) and r_g of SER (positive) with GYt were significant. Total leaf number and GLN influenced GYt negatively in the FD-experiment and positively in the CWI-experiment, but only r_g in both experiments and r_p in the CWI-experiment were significant. Correlations of GLN with many other characteristics in the FD-experiment were weak and insignificant except with SIPS, PH, DH and SER where both r_g and r_p were positively or negatively significant. In the CWI-experiment, however, GLN correlated significantly either positively or negatively with all characteristics measured except with PS where both r_g and r_p and with GYts and PH where r_p correlations were insignificant. Positive correlations of GLN with yield and its components and negative correlations with Chl and AUCPC-value may indicate its vital role in the yield formation process and reflection of plants to the damage caused by waterlogging stress. Several authors (Cai *et al.*, 1994; Cao *et al.*, 1994, 1995) have demonstrated the positive association of GLN with waterlogging stress tolerance in wheat. In both experiments, BY significantly correlated both genotypically and phenotypically with GYts, PS and KM and genotypically with GYms, SIPS and GPSI. In the CWI-experiment, BY correlated significantly and positively with all yield components except with PS and genotypically with GYts. Both r_g and r_p of Chl and AUCPC-value with SER were positive and significant; however, their correlations with all other characteristics were negative and significant except with PS, PH and DH and r_p with GYts. In several studies, waterloggimg has been shown to reduce grain yield through its negative impact on kernel weight, productive spikes and grains per spike (van Ginkel *et al.*, 1992; Cai *et al*, 1994, Boru, 1996). Strong negative influence of leaf chlorosis and area under chlorosis progress curve on the grain yield and its components has been reported in waterlogged wheat (van Ginkel *et al.*, 1992; Boru, 1996). The SSI index was negatively correlated genotypically and phenotypically with most of the characteristics measured in the CWI-experiment. Both genotypic and phenotypic correlations between STI index and all characteristics (except PH, DH and SER) were positive and significant. The significant negative and positive correlations

between SSI and STI, respectively, with most of the characteristics measured indicate that the indices that combined yields from both experiment could describe adequately the yield-based waterlogging sensitivity or tolerance in wheat. Genotypic and phenotypic correlation coefficients between the remaining characteristics followed patterns similar to those characteristics already explained.

Table 6.12. Genotypic (upper diagonal) and phenotypic (lower diagonal) correlation coefficients of various wheat characteristics in the freely drained experiment in 1999/2000

	GYt	GYmp	GYtp	BY	PS	GPS	KM	SIPS	GPSI	PH	DH	SER	TLN	GLN
GYt		0.837 ***	0.390 **	-0.028	-0.700 ***	0.635 ***	0.098	0.498 ***	0.741 ***	0.588 ***	-0.637 ***	0.511 ***	-0.394 **	-0.273 *
GYmp	0.592 ***		-0.178	0.346 **	-0.879 ***	0.680 ***	0.314 *	0.646 ***	0.872 ***	0.397 **	-0.636 ***	0.389 **	-0.268 *	-0.101
GYtp	0.817 ***	0.019		0.539 ***	0.225	-0.004	-0.354 **	-0.192	-0.136	0.395 **	-0.072	0.267 *	-0.136	-0.323 *
BY	0.242	-0.029	0.771 ***		0.355 **	0.096	-0.689 ***	0.266 *	-0.454 ***	0.292 *	0.640 ***	-0.046	0.080	0.111
PS	-0.113	-0.680 ***	0.346 **	0.395 **		-0.827 ***	-0.180	-0.744 ***	-0.875 ***	0.102	0.376 **	0.110	-0.158	-0.283 *
GPS	0.461 ***	0.673 ***	0.091	0.154	-0.758 ***		-0.410 **	0.917 ***	0.829 ***	0.100	-0.031	-0.097	0.180	0.364 **
KM	0.068	0.214	-0.069	-0.332 **	-0.114	-0.381 **		-0.437 ***	0.025	0.017	-0.683 ***	0.303 **	-0.394 **	-0.464 ***
SIPS	0.269 *	0.577 ***	-0.078	0.187	-0.565 ***	0.727 ***	-0.278 **		0.619 ***	0.090	0.156	-0.121	0.316 *	0.558 ***
GPSI	0.467 ***	0.622 ***	0.133	-0.050	-0.398 **	0.579 ***	-0.159	0.132		0.351 **	-0.595 ***	0.313 *	-0.209	-0.125
PH	0.267 *	0.335 **	0.093	0.181	0.037	0.069	0.085	0.102	0.168		-0.469 ***	0.931 ***	-0.865 ***	-0.735 ***
DH	-0.339 **	-0.566 ***	-0.015	0.409 *	0.289 *	-0.037	-0.535 ***	0.123	-0.405 **	-0.407 **		-0.708 ***	0.669 ***	0.629 ***
SER	0.246	0.355 ***	0.053	-0.061	0.037	-0.057	0.229	-0.086	0.211	0.841 ***	-0.693 ***		-0.912 ***	-0.784 ***
TLN	-0.056	-0.137	0.065	0.176	-0.134	0.187	-0.206	0.301 *	-0.221	-0.599 ***	0.562 ***	-0.766 ***		0.988 ***
GLN	-0.082	-0.054	-0.064	0.091	-0.125	0.185	-0.213	0.287 *	-0.065	-0.411 **	0.454 ***	-0.563 ***	0.877 ***	

[+] See Table 3 for abbreviations; *,**,*** significantly different from zero at 0.05, 0.01 and 0.001 levels of probability, respectively.

Table 6.13. Genotypic (upper diagonal) and phenotypic (lower diagonal) correlation coefficients of various wheat characteristics studied in the waterlogging experiment in 1999/2000

	GYt	GYmp	GYtp	BY	PS	GPS	KM	SIPS	GPSI	PH	DH	SER	TLN	GLN	CHL	AUCPC	SSI	STS
GYt		0.780 ***	0.675 ***	0.823 ***	0.278 *	0.463 ***	0.646 ***	0.606 ***	0.799 ***	0.116	-0.029	-0.071	0.277 *	0.708 ***	-0.881 ***	-0.870 ***	-0.961 ***	0.983 ***
GYmp	0.638 ***		0.064	0.934 ***	-0.314 *	0.708 ***	0.772 ***	0.904 **	0.723 ***	0.035	0.226	-0.463 ***	0.653 ***	0.838 ***	-0.906 ***	-0.943 ***	-0.844 ***	0.739 ***
GYtp	0.722 ***	-0.072		0.212	0.820 ***	-0.100	0.125	-0.099	0.417 ***	0.144	-0.304 *	0.428 ***	-0.324 *	0.145	-0.338 **	-0.278 *	-0.536 ***	0.708 ***
BY	0.707 ***	0.562 ***	0.410 **		-0.245	0.740 ***	0.882 ***	0.824 ***	0.605 ***	-0.056	0.229	-0.473 ***	0.668 ***	0.863 ***	-0.907 ***	-0.948 ***	-0.943 ***	0.758 ***
PS	0.358 **	-0.199	0.645 ***	0.113		-0.774 ***	-0.025	-0.500 ***	-0.058	-0.099	-0.564 ***	0.437 ***	-0.611 ***	-0.186	-0.131	-0.055	-0.162	0.289 *
GPS	0.371 **	0.571 ***	-0.028	0.383 **	-0.300 *		0.180	0.814 ***	0.777 ***	0.102	0.763 ***	-0.600 ***	0.825 ***	0.724 ***	-0.426 ***	-0.501 ***	-0.594 ***	0.419 ***
KM	0.441 ***	0.636 ***	-0.004	0.455 ***	-0.012	0.062		0.514 ***	0.256 *	-0.187	-0.283 *	-0.241	0.317 *	0.592 ***	-0.840 ***	-0.808 ***	-0.702 ***	0.595 ***
SIPS	0.413 **	0.827 ***	-0.206	0.382 **	-0.294 *	0.636 ***	0.334 **		0.647 ***	0.193	0.460 ***	-0.530 ***	0.812 ***	0.797 ***	-0.720 ***	-0.767 ***	-0.763 ***	0.504 ***
GPSI	0.694 ***	0.655 ***	0.312 *	0.505 ***	-0.018	0.602 ***	0.155	0.407 **		0.104	0.396 **	-0.275 *	0.421 **	0.667 ***	-0.676 ***	-0.752 ***	-0.781 ***	0.808 ***
PH	0.131	0.109	0.070	0.078	-0.037	0.140	-0.194	0.247 *	0.147		-0.141	0.659 ***	-0.363 **	-0.391 **	0.254	0.249	0.173	0.268 *
DH	0.014	0.158	-0.117	0.152	-0.272 *	0.513 ***	0.219	0.302 *	0.233	-0.048		-0.729 ***	0.809 ***	0.434 ***	0.017	0.016	-0.142	-0.085
SER	-0.110	-0.343 **	0.158	-0.299 *	0.209	-0.363 **	-0.178	-0.351 **	-0.148	0.518 ***	-0.590 ***		-0.919 ***	-0.785 ***	0.449 ***	0.552 ***	0.404 **	0.092
TLN	0.158	0.511 ***	-0.252	0.301 *	-0.410 **	0.565 **	0.220	0.613 ***	0.207	-0.172	0.574 ***	-0.743 ***		0.859 ***	-0.492 ***	-0.559 ***	-0.606 ***	0.107
GLN	0.514 ***	0.721 ***	0.018	0.509 ***	-0.122	0.575 ***	0.484 ***	0.668 ***	0.496 ***	-0.215	0.334 **	-0.604 ***	0.697 ***		-0.874 ***	-0.887 ***	-0.939 ***	0.575 ***
CHL	-0.700 ***	-0.747 ***	-0.234	-0.521 ***	-0.148	-0.349 **	-0.683 ***	-0.539 ***	-0.493 ***	0.183	-0.039	0.318 **	-0.375 **	-0.770 ***		-0.997 ***	0.993 ***	-0.785 ***
AUCPC-value	-0.649 ***	-0.741 ***	-0.172	-0.511 ***	-0.098	-0.407 **	-0.679 ***	-0.570 ***	-0.478 ***	0.169	-0.073	0.360 **	-0.436 ***	-0.793 ***	0.947 ***		0.989 ***	-0.779 ***
SSI	-0.820 ***	-0.510 ***	-0.604 ***	-0.548 ***	-0.277 *	-0.399 **	-0.352 **	-0.394 **	-0.562 ***	0.029	-0.116	0.233	-0.239	-0.603 ***	0.686 ***	0.658 ***		-0.900 ***
STI	0.901 ***	0.595 ***	0.631 ***	0.683 ***	0.310 *	0.297 *	0.415 ***	0.334 **	0.648 ***	0.212	-0.046	-0.017	0.083	0.349 **	-0.550 ***	-0.499 ***	-0.495 **	

+ See Table 3 for abbreviations; *,**,*** significantly different from zero at 0.05, 0.01 and 0.001 levels of probability, respectively.

CONCLUSIONS

The results indicated that there were considerable differences among genotypes in the genetic expression of waterlogging tolerance studied under both free drainage and continuous waterlogging conditions. Additive gene effects for waterlogging tolerance, as measured by GLN, Chl, and AUCPC-value and by the two yield-based indices (SSI and STI), were considerably more prevalent than non-additive effects. Relatively high estimates of heritability and predictability ratios as well as GCA:SCA ratios for waterlogging tolerance further confirmed the importance of general combining ability effects in the inheritance of waterlogging tolerance in bread wheat genotypes studied. The two waterlogging stress tolerant genotypes, PRL/Sara and Ducula, were found to be the best combiners for waterlogging stress tolerance and for most other agronomic characteristics and hence could be used to initiate a short-term breeding program to improve waterlogging tolerance in wheat.

Highly significant GCA and SCA effects were observed for most of the characteristics, including those relevant to waterlogging tolerance in both experiments, suggesting that both additive and non-additive gene effects were important in explaining the genetic variation for waterlogging tolerance and overall agronomic performance among the F_1 wheat progenies. These results imply that useful improvement in the tolerance and overall agronomic performance of wheat under waterlogging stress conditions would be attainable with a breeding system that in the long term could exploit both additive and non-additive gene effects simultaneously.

In this study, both genotypic and phenotypic correlations of GYt with all its components (except with PS) and STI index in both experiments and TLN and GLN in the CWI-experiment were significant and positive, while both correlations of GYt with CHl, AUCPC-value and SSI index in the CWI-experiment were significant and negative. The degree of dominance for waterlogging tolerance characteristics was estimated to be in the partial and complete dominance range. The significant heterotic response and SCA effects as well as the degree of dominance observed on several characteristics in some crosses under waterlogging stress suggest the

potential use of hybrid wheat in frequently waterlogged areas of wheat growing regions. The F_1 hybrid performance and SCA effects, however, failed to correlate with parental divergence measured using pedigree information and seed storage protein markers.

The genetic information generated from this study will assist decisions on breeding methodology and parental selection for a more extensive study of inheritance of waterlogging tolerance response in wheat. A better understanding of the genetic mechanisms of tolerance to waterlogging and associated stress will help to develop wheat genotypes having greater waterlogging tolerance and hence promote wheat production in frequently waterlogged wheat growing regions.

CHAPTER VII

SUMMARY

Analysis of genetic relationships in crop species can provide a relative measure of genetic diversity, an index of parental selection and structure for stratified sampling of populations. Seed storage proteins of 38 Ethiopian-grown and four advanced CIMMYT lines were fractionated by one-step sodium dodecyl sulfate-polyacrylamide gel electrophoresis (SDS-PAGE) to assess the composition of the three major endosperm proteins, determine the level of genetic diversity and search for the number of clusters among the genotypes of hexaploid wheat which is believed to be a relatively recent introduction to the Ethiopian highlands. The results indicated that there was a wide range of allelic variation in the composition of gliadins, low molecular weight (LMW-GS) and high molecular weight (HMW-GS) glutenin subunits among the different genotypes studied. A total of 82 polymorphic bands, i.e., 32 gliadins, 35 LMW-GS and 15 HMW-GS bands, were detected among the 42 genotypes. The mean protein-based genetic distance estimate was 0.609 unit with values ranging from 0.376 to 0.744 units. Over 80% of pairwise comparisons had genetic distance values between 0.440 and 0.700 units. Cluster analysis also resulted in five genetically distinct groups of genotypes.

Soil waterlogging is a serious environmental stress affecting wheat production in the high rainfall or irrigated areas with heavy clay Vertisols. Sixteen bread wheat genotypes were evaluated for their tolerance to prolonged transient and continuous waterlogging treatments. The results indicated that increased severity of soil waterlogging stress significantly reduced grain yields and growth of wheat; continuous waterlogging, in particular, resulted in greater damage to the plants in terms of most of the characteristics studied. The results also demonstrated that there were marked genotypic differences among the wheat genotypes studied for waterlogging tolerance. Ducula x1, PRL/Sara, HAR 604 and Vee/Myna were relatively tolerant whereas Et-13 and K 6290-Bulk were most sensitive to waterlogging stress. Under continuous waterlogging, grain yield was correlated positively with grains per spike and spikelet, kernel mass, biomass yield, number of green leaves on the main stem, the stress tolerance index, and negatively with percentage leaf chlorosis, area under chlorosis progress curve and the stress tolerance

index. Percentage leaf chlorosis, biomass yield, number of grains per spike and spikelet, and kernel mass accounted for over 88% of the total variation in the grain yield under continuous waterlogging. Heritability values of these characteristics and indices were also fairly large, indicating a promising gain from selection based on these characteristics.

Waterlogging of soils restricts crop performance by altering the soil mineral nutrient availability and uptake by roots. Two experiments were conducted to determine the effects of soil waterlogging on nutrient availability, and on the concentration and uptake of nutrients by wheat genotypes that differ in tolerance, and to assess the response of waterlogged wheat seedlings to foliar applications of selected nutrients. Root zone oxygenation was significantly depressed by the waterlogging treatments as indicated by significantly reduced soil redox potentials. All the 1*N* NH_4-acetate (pH 7.0) extractable mineral nutrient concentrations in the soil increased as waterlogging severity increased. A significant differential response of wheat genotypes to the waterlogging treatments was detected for several mineral nutrient concentration and uptake parameters. Compared to the tolerant genotypes, the sensitive genotypes appeared to accumulate more Fe, Mn, and Na although the concentrations were far below the level of toxicity reported for these nutrients, and less Cu, Zn, K, P and N with concentrations lower than the "critical" values previously reported for wheat. The results from the foliar application study indicated that waterlogging tolerance of wheat could be improved with the foliar application of Zn, Cu and P.

A study was undertaken to assess the combining ability effects, variance components, heterotic responses, heritability and correlations of waterlogging tolerance in a diallel cross involving five diverse bread wheat genotypes with contrasting tolerance response to waterlogging stress. The results showed that genotypic variability accounted for most of the variation among genotypes studied. Highly significant general combining ability (GCA) and specific combining ability (SCA) were observed for most of the characteristics studied, indicating that both additive and dominance gene effects were important in the inheritance of the waterlogging tolerance. GCA effects, however, were relatively more prevalent than SCA effects on most of the characteristics studied. The

tolerant genotypes PRL/Sara and Ducula were the best combiners for waterlogging stress tolerance and for most other agronomic characteristics studied. Relatively high estimates of heritability and predictability ratios were also observed for most characteristics relevant to waterlogging tolerance, confirming the importance of both additive and non-additive gene effects in controlling the waterlogging tolerance in wheat genotypes studied. The degree of dominance for waterlogging tolerance characteristics was estimated to be in the partial and complete dominance range. Under waterlogging conditions, grain yield correlated with genotypically and phenotypically positively with all its components, biomass yields, plant height, days to heading, number of green leaves on the main stem and stress tolerance index, and negatively with percentage leaf chlorosis, area under leaf chlorosis progress curve and stress susceptibility index. Substantial mid- and high- parent heterotic responses were observed for most characteristics in some crosses.

HOOFSTUK VII

OPSOMMING

Analise van genetiese verwantskappe in gewasse kan 'n relatiewe meting gee van genetiese diversiteit, 'n indeks vir ouer seleksie en struktuur vir gestratifiseerde monstering van populasies. Saad storings proteïene van 38 Etiopiese koring cultivars, en vier gevorderde CIMMYT lyne is gefraksioneer met een-stap natrium sulfaat poliakrielamied gel elektroforese (SDS-PAGE) om te toets vir die samestelling van die drie belangrikste endosperm proteïene, en vir die graad van genetiese diversiteit, en om te soek vir die aantal groeperings binne die genotipes van heksaploïede koring, wat 'n relatiewe onlangse introduksie is in die Etiopiese hooglande. Die resultate het getoon dat daar 'n groot reeks van alleliese variasie is in die samestelling van gliadiene, lae molekulêre gewig (LMW-GS) en hoë molekulêre gewig (HMW-GS) subeenhede. 'n Totaal van 82 polimorfiese bande is gevind, dit is 32 gliadiene, 35 LMW-GS en 15 HMW-GS, in die 42 genotipes. Die gemiddelde proteïen gebasseerde genetiese afstand skatting was 0.609 eenhede, met waardes wat wissel van 0.376 tot 0.744 eenhede. Meer as 80% van die paargewyse vergelykings het genetiese afstande tussen 0.440 en 0.700 eenhede gehad. Vyf duidelike genotipe groeperings was sigbaar.

Grond versuiping is 'n ernstige omgewings stremmings faktor wat koring produksie beïnvloed in hoë reenval of besproeiings areas met swaar klei Vertisol grond. Sestien brood koring genotypes is geëvalueer vir hulle toleransie vir voortgesette wisselende of permanente versuiping. Die resultate het aangetoon dat toename in versuipings stremming 'n betekenisvolle afname veroorsaak in opbrengs en groei van koring, deurlopende versuiping veral, het groot skade by plante veroorsaak in terme van alle gemete eienskappe. Die resultate het ook aangetoon dat daar groot genotipe verskille was tussen die cultivars. Ducula x 1 PRL/Sara, HAR 604 en Vee/Myna was redelik tolerant, terwyl Et-13 en K 6290-Bulk die mees sensitief was vir versuipings stremming. In deurlopende versuiping was graan opbrengs positief gekorreleer met korrels per aar en blompakkie, korrel massa, biomassa opbrengs, aantal groen blare per hoof halm, die stremmings toleransie indeks, en negatief met persentasie chlorose, area onder die chlorose ontwikkelings kurwe en die stremmings toleransie indeks. Persentasie blaar chlorose, biomassa opbrengs, aantal korrels per aar, en blompakkie en

korrel massa het 88% van die totale variasie in graan opbrengs onder deurlopende versuipings toestande verklaar. Oorerflikheids waardes van hierdie eienskappe en die indekse was redelik hoog, wat aandui dat daar goeie vordering sal wees vir seleksie vir hierdie eienskappe.

Versuiping van grond beperk gewas ontwikkeling deurdat dit grond mineraal beskikbaarheid en opname deur wortels beïnvloed. Twee proewe is gedoen om die effek van versuiping op voedingsstof beskikbaarheid te evalueer, en om die konsentrasie en opname van voedingstowwe deur genotipes met verskillende vlakke van toleransie te toets, en ook die respons van saailinge op blaar toedienings van sekere voedingsstowwe. Wortel sone oksiginering is betekenisvol onderdruk deur albei versuipings behandelings, soos aangedui deur 'n betekenisvolle afname in grond redoks potensiaal. Al die 1*N* NH_4 asetisaat (pH 7.0) eksraheerbare mineraal voedingstof konsentrasies in die grond het toegeneem soos versuiping vererger het. 'n Betekenisvolle differensiële reaksie van koring genotipes op behandeling is gesien vir verskillende mineraal voedingsstof konsentrasies, en opname parameters. In vergelyking met die tolerante genotipes, het die sensitiewe genotipes meer Fe, Mn en NA geakkumuleer, alhoewel die konsentrasies vêr onder toksiese vlakke was wat bekend is vir die voedingstowwe, en minder Cu, Zn, K, P en N geakkumuleer met konsentrasies minder as die "kritiese" waardes wat voorheen vir koring gerapporteer is. Die resultate van die blaar toedienings studie het aangetoon dat versuipings toleransie in koring verbeter kan word deur die blaar toediening van Zn, Cu en P.

'n Studie is gedoen om kombineervermoë, variansie komponente, heterose, en korrelasies van versuipings toleransie in 'n diallele kruis met vyf diverse brood koring genotipes met kontrasterende toleransie vir versuipings stremming. Die resultate het getoon dat genotipiese variabiliteit verantwoordelik was vir meeste variasie tussen die genotipes. Hoogs betekenisvolle algemene kombineervermoë (GCA) en spesifieke kombineervermoë (SCA) is gesien vir meeste eienskappe, wat aandui dat beide additiewe en dominansie geen effekte belagrik is vir die oorerwing van versuipings toleransie. GCA effekte was egter relatief meer belangrik as SCA vir meeste van die eienskappe bestudeer. Die tolerante genotipes PRL/Sara en Ducula was die beste

kombineerders vir versuipings toleransie en vir meeste ander agronomiese eienskappe bestudeer. Relatiewe hoë oorerflikhede en voorspelbaarheids verhoudings is gesien vir meeste eienskappe relevant vir versuipings stremmings toleransie, wat bevestig die belangrikheid van beide additiewe en nie-additiewe geen effekte in die beheer van versuipings toleransie in koring genotipes bestudeer. Die graad van dominansie vir versuipings tolerante eienskappe is vasgestel in die gedeeltelike of volledig dominante reeks. Onder versuipings toestande, het graan opbrengs genotipies en fenotipies gekorreleer met alle komponente van opbrengs, en met biomassa opbrengs, plant hoogte, dae tot aarstoot, aantal groen blare op die hoof halm en stremmings toleransie indeks, en negatief met persentasie blaar chlorose, area onder blaar chlorose ontwikkelings kurwe en stremmings vatbaarheid indeks. Betekenisvolle mid- en hoër ouer heterotiese respons is gesien vir meeste eienskappe in sommige kruisings. .

CHAPTER VIII

CONCLUSIONS AND RECOMMENDATIONS

Wheat is one of the principal cereal crops grown in Ethiopia. Genetic diversity in the available gene pool is the foundation for any crop improvement program because it helps to avoid crop vulnerability to pests and abiotic stress and to ensure continued selection gains. Electrophoresis of seed storage proteins provides protein-banding patterns, which can be used to detect the level of variation among genotypes. From the study of seed storage protein compositions, it became apparent that there was a wide range of variation among the Ethiopian-grown bread wheat genotypes in the composition of gliadins, LMW-, and HMW-GS of proteins. The level of diversity within the adapted Ethiopian bread wheat gene pool was fairly large, despite the common belief that the introduced hexaploid wheat in Ethiopia is narrow in its genetic diversity (Gebre-Mariam, 1991). Estimates of genetic distance based on seed storage protein banding patterns were quite extensive with values ranging from 0.376 to 0.744 units and a mean of 0.609 unit. Cluster analysis also separated the 42 bread wheat genotypes into five genetically distinct groups. Relatively large genetic diversity in the adapted Ethiopian-grown bread wheat gene pool is largely attributed to the widespread use of germplasm from CIMMYT, which are known for their wide genetic bases. It is therefore suggested that cross-hybridizing parental genotypes that are genetically distant from different clusters could generate populations with desirable means and large genetic variance thereby improving the efficiency of the breeding program in the development of new cultivars. Moreover, application of the seed storage protein electrophoretic technique and the results reported herein would be of great importance to the Ethiopian bread wheat improvement program in facilitating accurate cultivar identification, proper germplasm management, seed certification, quality control and registration of new cultivar releases.

Soil waterlogging, due to temporary, transient or continuous ponding of excess surface water, is a widespread environmental stress affecting crop production in high rainfall and irrigated areas throughout the world. The incidence of waterlogging stress in the central and eastern African highlands, particularly in the Ethiopian highlands, is serious because of the widespread occurrence of poorly drained heavy clay Vertisols and a low

evaporative demand during crop growing season. The results from the study on the response of bread wheat genotypes to the different waterlogging stress treatments demonstrated that large differences in the tolerance to prolonged waterlogging exist among the bread wheat genotypes, as indicated by significant genotype x waterlogging interactions for most of the characteristics studied. Ducula x1, PRL/Sara, HAR 604 and Vee/Myna were relatively tolerant whereas Et-13 and K6290-Bulk were most sensitive to waterlogging stress. Under continuous waterlogging, the percentage leaf chlorosis, biomass yield at maturity, grains per spike and kernel mass correlated highly significantly with, and accounted for over 88% of the total variation in the grain yields. The yield-based stress susceptibility and tolerance indices also correlated strongly with the different components of yield and with the most relevant characteristics of tolerance such as number of green leaves, and percentage leaf chlorosis at heading and the area under chlorosis progress curve. Heritabilities of these characteristics and indices were also large, promising a substantial gain from selection based on theme. It is therefore recommended that the use of percentage leaf chlorosis at heading, biomass yield at maturity, number of grains per spike and kernel weight as selection criteria would facilitate development of waterlogging stress tolerant cultivars in wheat.

Waterlogging of soil restricts crop performance by altering soil mineral nutrient availability and uptake by roots. The mineral composition of waterlogged wheat depends largely on soil aeration and O_2 availability. A study that was conducted to assess the effects of different degrees of waterlogging on nutrient availability, and on nutrient concentration and uptake by wheat genotypes differing in tolerance indicated that root zone oxygenation was significantly depressed by the waterlogging treatments as indicated by lower redox potentials. Soil waterlogging increased all mineral nutrient concentrations in the soil, but the effect was more pronounced for the Fe, Mn, K and Na -concentrations. The results have demonstrated that there was a considerable difference between waterlogging-sensitive and -tolerant wheat genotypes in their nutrient accumulation and uptake ability under waterlogging conditions. Sensitive genotypes accumulated more Fe, Mn, and Na although the concentrations were far below the level of toxicity reported for these nutrients, and less Cu, Zn, K, P and N than the tolerant genotypes. The concentrations of Cu, Zn, K, P and N nutrients appeared to be lower

than the "critical" values previously reported for wheat (Melsted *et al.*, 1969 Bergmann, 1992). The damaging effects of waterlogging on wheat therefore were not due to Fe, Mn, or Na toxicity but can rather be attributed to the decreasing nutrient uptake due to an O_2-deficiency in the root zone, particularly P- and Zn-deficiencies. The results from a foliar nutrient application study to supplement Cu, Zn and P indicated that there was a nutrient-induced improvement in waterlogging tolerance and, therefore, the adverse effects of waterlogging could be offset to some extent by the foliar application of deficient nutrient. Zn-deficiency is most common in the cool and wet highland Vertisols with high montmorillonite clay content, high pH-values, and high phosphate and organic matter contents (Bergmann, 1992). It is therefore suggested that in a breeding program aimed at improving waterlogging tolerance in wheat, selection of genotypes with greater ability to overcome the waterlogging–induced nutrient deficiencies, particularly P- and Zn-deficiency, could improve wheat productivity on waterlogged soils. Further studies are, however, necessary to clearly define the effect of P and Zn nutrition on the reduced growth resulting from waterlogging and also to establish the mode of genetic inheritance of tolerance to P- and Zn-deficiency associated with waterlogging in wheat.

The results from an analysis of diallel crosses of five diverse bread wheat genotypes with contrasting tolerance response to waterlogging stress indicated that both general combining ability (GCA) and specific combining ability (SCA) were highly significant for most of the characteristics studied, indicating that both additive and dominance gene effects were important in the inheritance of the waterlogging tolerance. However, GCA effects were relatively more prevalent than SCA effects on waterlogging tolerance as measured by the number of green leaves on main stem, percentage leaf chlorosis, and area under chlorosis progress curve as well as by the yield-based indices. Relatively high estimates of heritability and predictability ratios as well as GCA: SCA ratios for waterlogging tolerance further confirmed the importance of additive gene effects than non-additive effects in the inheritance of waterlogging tolerance in bread wheat genotypes studied. The two waterlogging stress tolerant genotypes, PRL/Sara and Ducula, were found to be the best combiners for waterlogging stress tolerance and for most other agronomic characteristics and hence could be used to initiate short-term

breeding program to improve waterlogging tolerance in wheat. However, since the importance of both additive and non-additive gene effects in the inheritance of waterlogging tolerance and most other agronomic characteristics were implicated by the highly significant GCA and SCA effects, most useful improvement in the tolerance and overall agronomic performance of wheat under waterlogging stress conditions would be attainable with a breeding system that in the long term could exploit both additive and non-additive gene effects simultaneously. The degree of dominance for waterlogging tolerance characteristics was estimated to be in the partial and complete dominance range. The significant heterotic response and SCA effects as well as the degree of dominance observed on several characteristics in some crosses under waterlogging stress conditions suggest the potential use of hybrid wheat varieties in frequently waterlogged areas of wheat growing regions. The F_1 hybrid performance and SCA effects, however, failed to correlate with parental divergence measured using pedigree information and seed storage protein markers.

The genetic information generated from this study will assist decisions on developing a breeding methodology and parental selection for more extensive studies of inheritance of waterlogging tolerance response in wheat. A better understanding of the genetic mechanisms of tolerance to waterlogging and associated stress will help to develop wheat genotypes having greater waterlogging tolerance and hence promote wheat production in frequently waterlogged wheat growing regions.

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