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Heritability of Waterlogging Tolerance in Wheat.

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HERITABILITY OF WATERLOGGING TOLERANCE IN WHEAT

A Dissertation

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

in

The Department of Agronomy

by

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To Etleva, Olta, and Egnatia.

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ABSTRACT

Waterlogging stress is one of the factors that limits wheat yield. Previous investigations indicated that genetic variation exists, however, heritability of waterlogging tolerance in wheat has not been specifically studied. The objectives of this study were: (1) to study the effect of waterlogging on yield and yield components of soft red winter wheat; (2) to estimate yield losses from waterlogging; (3) to estimate heritability of yield and yield components under waterlogging stress in early generations of wheat, and (4) to provide selection criteria for waterlogging tolerance in wheat breeding. Linear reduction in yield and yield components was observed as a result of 0, 10, 20, and 30 days of waterlogging. Average yield losses from waterlogging, evaluated in a field experiment were 44%. This reduction was mainly due to a decrease in tiller number and kernels/head. Screening of wheat genotypes identified the potential for waterlogging tolerance in breeding material. Genotypes Terral LA 422, Shelby, and Pioneer 26R61 were the most waterlogging tolerant. Some of the high yielding genotypes under non-flooded conditions, such as Coker 9663 and FFR 502W, had low tolerance to waterlogging. Restricted maximum likelihood (REML) estimation of additive and dominance variance components were obtained from 80 related F_2 families. Compared to the traditional quantitative genetic designs, this method provides estimates of genetic variance components without any restriction in mating design. Narrow sense heritabilities estimated on a per plot basis were high for kernel weight and chlorophyll content. Early generation selection for waterlogging tolerance for yield would not be efficient. Heritability of yield was low and its standard error was high. Strong genetic correlations

were observed between yield and kernel weight; and yield and tiller number. Selection indices were constructed to make use of a strong genetic correlation of yield with some yield components with high values of heritability. A maximal improvement of 17% is expected in yield, as a result of selection based on yield-kernel weight-tiller number index. At least three cycles of selection would be needed to produce waterlogging tolerant populations by applying this selection index.

INTRODUCTION

Waterlogging stress is one of the factors limiting wheat yield. A watertable at or close to the soil surface has been shown to reduce grain yield of winter wheat by about 20% (Belford, 1981, Cannell et al. 1984). About 12% of agricultural soils in the U.S.A. are affected by excess soil water (Boyer, 1982).

Wheat along the Gulf-coast and other regions of the lower Mississippi valley is frequently subjected to waterlogging due to heavy rainfall and inadequate soil drainage. In this region, waterlogging affects winter wheat due to high rainfall, especially during the first months of growth (Musgrave, 1994). Waterlogging stress is not restricted to areas of heavy rainfall but occurs periodically in arid regions that are irrigated (Kozlowski 1984). It has been estimated that about 10 million hectares of land planted with wheat have medium to severe waterlogging stress (Boru, 1996).

Waterlogging reduces shoot and root growth, dry matter accumulation and final yield (Trought and Drew, 1980a ; Kozlowski, 1984; Drew, 1991; Huang et al., 1994; Musgrave, 1994). It depresses absorption of water (Gales et al., 1984; Waters et al., 1991) and reduces photosynthesis (Musgrave, 1994; Huang et al., 1994). Plants may also suffer from nutrient deficiencies and leaching of nutrients, and the dilution of ions in waterlogged soil (Drew, 1991; Huang et al., 1994). Grain yield is greatly reduced by waterlogging during the period from the stem elongation to ear emergence (Gardner and Flood, 1993). Generally it has been suggested that waterlogging causes more damage if it occurs early in the life of the plant with the germination phase being especially susceptible (Trought and Drew, 1980b; Belford, 1981; Gardner and Flood, 1993).

There is some evidence of genotypic differences in tolerance to waterlogging in wheat. Davies and Hillman (1988) demonstrated variation in vegetative growth and yield under continuous flooding of four week old plants of various wheat species. Van Ginkel et al. (1991) identified 14 waterlogging tolerant spring wheat lines by screening a large number of genotypes. Sayre et al. (1994) using a five week waterlogging treatment identified six tolerant genotypes in terms of number of tillers, leaf chlorosis, senescence, fertility, grain yield and kernel weight. Other varietal studies for waterlogging stress in wheat have been reported by Thomson et al. (1992), Huang et al. (1994), and Musgrave and Ding (1998). The presence of a few genes in grasses for waterlogging tolerance was reported by Mujer et al. (1993), Taeb et al. (1993), and Boru (1996).

There are no specific reports on heritability of waterlogging tolerance in wheat. However such information is important considering the severe damages in many areas of the world. In the absence of a reliable marker, different morphological and physiological traits have been used in genetic studies for waterlogging tolerance (Taeb et al., 1993; Boru, 1996). Most of these traits are quantitative and highly influenced by the environment. By studying the heritability of the traits under waterlogging stress we can separate the influence of non-genetic from the genetic factors accounting for waterlogging tolerance. Furthermore, the heritability of traits influenced by waterlogging provides estimates of selection response to be used for the improvement of the breeding population for waterlogging tolerance. Therefore, the objectives of this research were: 1) to study the effect of waterlogging on yield and yield components of soft red winter wheat; 2) to estimate losses in yield and other traits from waterlogging stress and

determine their relative importance as indicators of waterlogging tolerance; 3) to estimate the heritability of waterlogging tolerance in early generation of wheat for yield and other quantitative traits, and 4) to provide selection criteria for waterlogging tolerance in wheat breeding.

1. HERITABILITY IN PLANT BREEDING

1.1 Statistical Approach for Heritability

The phenotypic value of quantitative traits is a result of genotypic, environmental and genotype-by-environment (GE) interaction effects. To estimate the breeding value for a quantitative trait we need to know the contribution of the genotype to the phenotypic value, or more exactly that part of genotypic variability that expresses the mean effects of genes, or the additive variance. This contribution is constant because genes do not change from year to year or from location to location, whereas the contribution of environments to the observed values is variable due to unpredictable environmental factors, such as temperature, rainfall, etc. The percentage of total phenotypic variance that is due to the genotypic effects is related to the concept of heritability. Estimation of heritability is important because traits with higher values of heritability can be improved more rapidly than traits with lower heritability.

1.1.1 Concepts and Implications

Heritability of a trait is a measure of the relative importance of genetic effects. There are two types of heritability: broad sense heritability and narrow sense heritability.

Broad sense heritability (H^2) is the ratio of genetic variance (σ_G^2) to the phenotypic variance (σ_P^2): $H^2 = \sigma_G^2 / \sigma_P^2$. During reproduction genes segregate and come together in new combinations exhibiting intra-allelic interactions (degree of dominance) and inter-allelic interactions (epistasis). The differences between the actual effects of genes in combination and their mean effect in the population are expressed in terms of dominance and epistasis.

Narrow sense heritability (h^2) is the ratio of additive genetic variance to phenotypic variance: $h^2 = \sigma_A^2 / \sigma_P^2$. It indicates the relative importance of genetic additive effects in determining the phenotypic variance. This type of heritability is more meaningful than the broad sense heritability because it considers only that part of genetic variance that has breeding value, i.e., that is transmitted into the progeny material (σ_A^2). Use of narrow sense heritability is important in early generation of selection, such as F_2 , F_3 , where σ_D^2 is an important part of genetic variance.

1.1.2 Genetic Variance Components

A model characterizing the variability for a set of phenotypic observations is needed to define genetic and non-genetic variance components related to heritability. The simplified linear additive model described by many authors (Falconer, 1989; Wricke and Weber, 1986; Nyquist, 1991) for the phenotypic values is:

$$P_{ij} = \mu + G_i + E_j + (GE)_{ij} \quad [1]$$

where P_{ij} = phenotypic value of the i th genotype in the j th environment, μ = population mean, G_i = genotypic effect of the i genotype, E_j is the environmental effect of the j th environment, $(GE)_{ij}$ is the interaction effect of the i th genotype with j th environment.

The environmental effect E_j , is due to micro-environmental and macro-environmental effects. The micro-environmental effects are differences affecting the plant during its life span. They are called unclassifiable environmental effects, and are lumped into residual component of variance. Macro-environmental effects are due to particular sources of variation, such as replications, location, etc, their effect is measured by environmental variance σ_E^2 , and they are called classifiable environmental effects.

Genotype by environment interaction (GE)_{ij} occurs because different genotypes react differently to changes in environments. Therefore, GE interaction is a result of non-parallel response of genotypes across environments. Testing of a number of genotypes in a series of environments provides the estimate of GE interaction, that is important in selection of target environments (Collaku, 1991; Harrison et al., 1996; Kang and Magari, 1996). However, environmental and GE interaction variance can not be used for selection, since they are not constantly present in the progeny material (Allard and Bradshaw, 1964; Wricke and Weber, 1986).

Based on model [1] and the assumption that all covariances between the effects in the model are zero, the phenotypic variance (σ^2_p) would be:

$$\sigma^2_p = \sigma^2_G + \sigma^2_{GE} + \sigma^2_E \quad [2]$$

Where, σ^2_G is the genotypic variance composed of the following components

$$\sigma^2_G = \sigma^2_A + \sigma^2_D + \sigma^2_{AA} + \sigma^2_{DD} + \sigma^2_{AD} + \sigma^2_{AAA} + \dots \quad [3]$$

The additive variance component (σ^2_A) measures the mean genotypic effect that is expected in the selected material. Under no selection this variance component is assumed to be constant for a given genetic material, therefore it is called the variance that measures the breeding value (Falconer, 1989).

The dominance variance (σ^2_D) measures deviations of genotypic values from their additive effects due to interactions between alleles in the same locus. Dominance effect is associated with heterozygosity and is reduced as heterozygosity decreases.

Epistatic variance components σ^2_{AA} , σ^2_{DD} , σ^2_{AD} , etc., are due to interaction of non-allelic genes in the form additive-by-additive; dominance-by-dominance; additive-

by-dominance; etc. The amount of variability estimated by the epistatic variance components is usually small and is assumed to be zero (Wricke and Weber, 1986; Nyquist, 1991).

Genetic variance components are estimated from the covariance between relatives. This is done by measuring phenotypic values of relatives in a population. Relatives may be descendants in different generations, known as lineal relatives, such as parent-offspring, etc., or have one or more common ancestors, the relatives being in the same or different generations, known as collateral relatives, such as half-sibs, full-sibs, etc. The phenotypic covariance between two random individuals related in a particular way has been proved to be the sum of genotypic covariance, the covariance of their GE effects, and the covariance between their environmental effects. (Cockerham, 1963; Kempthorne, 1969). By use of proper experimental design and randomization, these three covariances can be estimated separately (Nyquist, 1991). Under certain assumptions, such as: Mendelian inheritance, two or more alleles at each locus, free recombination (no linkage), no maternal effects, large population size, random mating, and random and unrelated parents; the genetic covariance can be expressed as a linear function of genetic variance components (Cockerham, 1963):

$$\text{Cov}(G_X G_Y) = r\sigma_A^2 + u\sigma_D^2 + r^2\sigma_{AA}^2 + u^2\sigma_{DD}^2 + ru\sigma_{AD}^2 + r^3\sigma_{AAA}^2 + r^2u\sigma_{AAD}^2 + \dots [4]$$

where $r = 2f_{XY}$, and f_{XY} is the coefficient of coancestry between the two relatives, X and Y; and $u = f_{AC}f_{BD} + f_{AD}f_{BC}$, is the double coancestry coefficient, where A and B are the parents of X, and C and D are the parents of Y. The value of coancestry coefficients can be computed for any pedigree by using the procedures described by Falconer (1989),

Wricke and Weber (1986), or Kang (1994). Convenient computer software, such as Proc inbreed of SAS (1996) can be used to calculate coancestry coefficients, especially when many related individuals are included in the study.

Assuming no epistatic interaction the model for genotypic covariance among relatives simplifies to:

$$\text{Cov}(G_x G_y) = r\sigma_A^2 + u\sigma_D^2 \quad [5]$$

Assuming non-inbred and unrelated ancestors for the half-sib relatives, $r = 1/4$ and $u = 0$, the genotypic covariance among half-sibs is:

$$\text{COV}_{HS} = 1/4\sigma_A^2 \quad \text{or} \quad \sigma_A^2 = 4\text{COV}_{HS} \quad [6]$$

Under the assumptions of $r = 1/2$ and $u = 1/4$ for the full-sib relatives, the genotypic covariance among full-sibs is:

$$\text{COV}_{FS} = 1/2\sigma_A^2 + 1/4\sigma_D^2 \quad [7]$$

Equations (5) and (7) are useful under strict mating designs and require a number of restrictions for the way half and full sibs are produced.

1.1.3 Mating Designs

Various mating designs are used to create different kinds of relatives and to estimate their genetic variance components (Cockerham, 1963; Wricke and Weber, 1986; Hallauer and Miranda, 1988). Some simple designs, such as topcross and polycross designs estimate only additive variance component. Another simple one factor mating design is that of full-sib families used in plant species with bisexual individuals (Nyquist, 1991). When dominance variance is not negligible, such as in early segregating generation F_2 , F_3 that have a degree of heterozygosity, more complex mating designs are

required to estimate both additive and dominance variance (Comstock and Robinson, 1948; Hallauer and Miranda, 1988). Such designs include: (1) nested design, also called Design I by Robinson et al. (1949) or design A/B or B/A (Cockerham, 1963); (2) factorial design, A x B design or Design II according to Robinson et al. (1949); (3) diallel design or A x A design.

In nested design, a sample of m males is chosen randomly and each m_i male is crossed with f_j randomly chosen females, each set of females being different from each other, and the progenies are tested in different replications. In the factorial design two different sets of parents (male and female) are used, and each male is crossed with the same females. Since the total number of crosses is mf , m and f can not be both large. In diallel only one group of parents is used, as both males and females. When the number of parents is large, the number of crosses increases rapidly.

All of these mating designs can readily be analyzed by standard statistical procedures and provide components of variance that can be translated into covariances of relatives. In almost all the cases the genetic variance components are estimated by the least squares technique or ANOVA. This method of estimating genetic variance components has some disadvantages. When parents involved in crosses have some kind of relationships the mating designs are no longer useful. In these cases that are common in plant breeding, variance components of additive and dominance effects can not be estimated using ANOVA because of different coancestry coefficients among any two crosses. Negative variance component estimates may result based on the procedure of equating observed mean squares to expressions describing their expected values of the

variance components. Finally, when the data are unbalanced the properties of the estimators are poorly understood (Searle, et al., 1992).

Hayman (1960) proposed maximum likelihood (ML) methods to improve estimation of genetic variance components. Mixed model equations (Henderson, 1975, Harville, 1977) provide ML estimators of variance components. Such estimators do not place any special demand on the mating design and they can be used for any pedigree. Bernardo (1994) used mixed model approach to estimate additive and dominance genetic variance components of a single cross corn population derived from parental inbreds that were related. Bromley et al. (2000) used a similar procedure to estimate total genetic variance in corn, from F_1 performance with pedigree relationships among inbred lines.

1.1.4 Estimation of Heritability

The most common methods of estimating heritability use the relationship among relatives, either collateral (half-sib families) or lineal (parent-offspring). Other methods use selection results in terms of realized heritability (Wricke and Weber, 1986, Falconer, 1989; Nyquist, 1991).

In estimating heritability of a population we need to define the environment(s) for which the estimate is valid. After the environments have been defined we can define genotypic and additive values of genotypes. The observed (phenotypic) variance can be that of individuals in a population, the phenotypic means of families or relatives, etc. Based on the way phenotypic variance is measured, heritability may be expressed on individual basis, or on a plot mean basis.

Another important factor influencing heritability is genotype by environment interaction. Its magnitude increases as the magnitude of environmental differences increases (Comstock and Moll, 1963; Gauch and Zobel, 1988, Kang and Magari, 1996). Considering the general linear model [1] and equations [2] and [3], narrow sense heritability on plant basis would be:

$$h^2 = \sigma_A^2 / [\sigma_A^2 + \sigma_D^2 + \sigma_{GE}^2 + \sigma^2] \quad [8]$$

In the case where phenotypic variance of i families (genotypes) is based on the mean of plots for r replications and l environments, narrow sense heritability would be:

$$h^2 = \sigma_A^2 / [\sigma_A^2 + \sigma_D^2 + \sigma_{GE}^2 / l + \sigma^2 / r l] \quad [9]$$

Another way to estimate heritability, is the use of lineal relatives or parent-offspring regression (Wricke and Weber, 1986; Falconer, 1989). Regression of phenotypic values of offspring on that of either one parent or the mean of its two parents is used:

$$h^2 = 2 b_{XY} \quad [10]$$

where b_{XY} is the regression coefficient of phenotypic values of a given quantitative trait of offspring Y on parent X. The genotypic covariance between a single parent and an individual offspring produced by random mating within the population is equal to one half of the additive variance of the population (assuming no epistatic interaction).

Genotypic covariance can be evaluated based on an individual or mean of individual offspring. The mean of offsprings is used more often to reduce the sample error in estimating genotypic covariance (Nyquist, 1991). The regression coefficient is multiplied by two to obtain an estimate of narrow sense heritability.

Based on the fact that $b_{XY} = \text{Cov}_{XY}/\text{Var}_X$, heritability on individual plant basis will be calculated as:

$$h^2 = 2 \text{Cov}(X, Y)/\sigma_p^2 \quad [11]$$

where σ_p^2 is the phenotypic variance among single individual plants.

When the mean of two parents is used instead of a single parent, estimates of heritability in [11] changes in:

$$h^2 = \text{Cov}(X, Y)/\sigma_p^2 \quad [12]$$

The covariance remains the same as in [11], since it is simply the mean of the covariance of the female parent with the offspring and the covariance of the male parent with the offspring and in plants these two covariances are generally equal (Hanson, 1963; Cockerham, 1963). The phenotypic variance, which is the phenotypic variance of the mean of the parents is one half of that of a single parent, therefore, to obtain the narrow sense heritability we do not multiply by two, as in the case when only one parent is used.

Heritability estimated with parent-offspring method does not require the assumption for linkage (Cockerham, 1963) and the parents do not have to be random members of the population. The main problem with this method arises when parents are measured in the same environment as offspring. If the two environments are two different years in the same location, the parent-offspring covariance is biased by genotype by environment interaction components (Comstock and Robinson, 1948; Vogel et al., 1980). On the other hand very different environments for parents as compared to offspring might influence in very different phenotypic variances of the offspring relative to the phenotypic variance of parents. By regressing polycross-progeny means on

parental means evaluated in the same single location, Buckner et al. (1981) obtained large parent-offspring heritabilities, whereas when parental and offspring values were obtained in different locations, greatly reduced parent-offspring heritabilities resulted. Frey and Horner (1957) proposed the standardization of the phenotypic variances of both parents and offspring in self-fertilizing crops. This way phenotypic variances of parents and offspring would be equal except a scaling factor.

In self-fertilizing crops, the most common use of parent-offspring method is the regression of F_3 family means in one environment on F_2 individuals in the previous year in the same location. The heritability in this case would be equal to $h^2 = \text{Cov}(X, Y) / \sigma^2_{P(F_2)}$. The additive fraction of the parent-offspring regression increases with inbreeding (Mather and Jinks, 1982; Narain, 1990). Different methods to correct heritability estimates by inbreeding coefficient are proposed (Prest et al., 1983; Grumet et al., 1985).

Realized heritability is another heritability estimate calculated from the results of selection. It is available only if selection has occurred and can be used to predict the change in the next few generations. Hill (1972a, 1972b) described four methods to estimate realized heritability: 1) regression of individual generation responses on individual selection differentials; 2) regression of cumulative response on cumulative selection differential measured at each generation; 3) the ratio of total response to total selection differential; 4) maximum likelihood method. In self-fertilized crops, realized heritability is generally calculated as the ratio of differences between the means of the high and low F_3 families to the corresponding difference of the selected individuals in the F_2 generation (Marsh et al., 1985; Wang et al., 1989).

Most heritability estimates are biased upward due to genetic or environmental factors (Hanson, 1963; Cockerham, 1963; Nyquist, 1991). Although in some cases bias can not be avoided in estimating heritability, it is important to know what bias terms are present. Heritability estimates are biased due to some additive by additive epistatic component of variance in the numerator that is difficult to separate from the additive variance. Although plant breeders usually work based on the assumption of no epistatic interaction, this is not always true, especially when working with self-fertilized crops when covariances of inbred relatives are estimated in the same or different generations (Cockerham, 1963; Harris, 1964; Cornelius, 1975). Due to inbreeding status, heritability estimates are biased not only for additive by additive component, but for dominance, and for additive by dominance components (Cockerham, 1963).

Many heritability estimates are also biased upward due to environmental factors because they are not estimated relative to a target population of environments (Hanson, 1963; Nyquist, 1991). Estimation of heritability is not always based on a number of locations and years, in order to account for genotype by environment interaction. This is the case especially in early generation when the genetic material is large (Fehr, 1987).

1.1.5 Standard Errors of Heritability

In estimating heritability, it is important to measure the precision of heritability estimators. Heritability as a ratio of variance component estimates is a point estimate (Snedecor and Cochran, 1980; Casella and Berger, 1990). The standard error of heritability and confidence interval associated with it are a measure of the precision of heritability estimates.

The development of accurate measures of precision for heritability estimators depends on their distribution. Kempthorne (1969) gave the formula for the approximate standard error of heritability estimated as an interclass correlation. Pesek and Baker (1971) computed the standard error of a heritability estimate, when locations and years were cross-classified. Graybill and Wang (1979) described methods for setting approximate confidence intervals on heritability on an individual progeny basis.

The approximate standard error (SE) for heritability is:

$$SE(h^2) = SE(\hat{H}) = SE(\hat{\sigma}_F^2) / \hat{\sigma}_P \quad [13]$$

where $\hat{\sigma}_F^2$ is the family genetic variance estimated in a specific mating design.

The interval $\hat{H} \pm SE(\hat{H})$ implies that $\hat{H}$ is distributed according to a symmetric distribution, e.g., Student's or normal. The distribution of heritability, particularly that for a low value tends to be asymmetrical (Knapp et al., 1985; Nyquist, 1991). Therefore, the distribution of H is misinterpreted because the F-distribution of the ratio of variances in heritability estimate is left-skewed. Based on F distribution, Knapp et al. (1985) gave exact confidence interval of heritability as:

$$P\{1 - [(M_1/M_2)F_{1-\alpha/2, df_2, df_1}]^{-1} \leq 1 - (\theta_2/\theta_1) \leq 1 - [(M_1/M_2)F_{\alpha/2, df_2, df_1}]^{-1}\} = 1 - \alpha \quad [14]$$

where M_1 is the family mean square of an experiment with r replications in l

environments with an expectation $\theta_1 = \sigma_\epsilon^2 + r\sigma_{FE}^2 + lr\sigma_F^2$, and M_2 is the mean square of the family by environment interaction with an expectation $\theta_2 = \sigma_\epsilon^2 + r\sigma_{FE}^2$, and $F_{1-\alpha/2, df_2, df_1}$ denotes the value of F, such that the probability of exceeding this value is $1 - \alpha$.

Reciprocal F, i.e., $F_{\alpha/2, df_2, df_1}$ can be calculated from the equation $F_{1-\alpha/2, df_2, df_1} = 1/F_{\alpha/2, df_2, df_1}$.

Based on the expectations for M_1 and M_2 , the true value of heritability in [14] is $1-(\theta_2/\theta_1)$. This method used for setting exact $(1-\alpha)$ confidence interval on heritability is not restricted to a particular linear model, but it does require that heritability estimate be expressed as a function of two mean squares and it is used either for broad or narrow sense heritability.

Knapp (1985) extended the idea of constructing exact confidence intervals for the two factor mating design. Tai (1979) gave the confidence interval for the expected response to selection. Hanson (1989) gave an alternative form for calculating standard error of heritability and expected selection response. Bridges et al. (1991) described an exact and approximate standard error for expected selection response using a normal approximation.

To obtain useful heritability estimates, apart from the mating design, adequate sampling is necessary (Pederson, 1972; Knapp et al., 1987). Generally, small experiments do not provide a representative sample for heritability estimates, but very large experiments may not provide estimates of sufficient reliability to justify their cost.

Standard error of any parent-offspring estimate of heritability is simply the standard error of the linear regression coefficient (s_b). For a single parent, $s(\hat{h}^2) = 2s_b$, and for the mean of two parents $s(\hat{h}^2) = s_b$. Using the standard error s_b , a symmetric confidence interval can be constructed (Snedecor and Cochran, 1980; Steel and Torrie, 1981; Casella and Berger, 1990).

1.1.6 Prediction of Selection Response

Heritability concept is commonly related with prediction of genetic gain from selection or expected selection response (Hanson, 1963; Falconer, 1989; Narain, 1990; Nyquist, 1991). The prediction of expected gain from selection is a regression problem to relate the genotypic value Y in the generation of study to the phenotypic value of the selection unit X . Selection response (R) is:

$$R = b_{YX}S = [\text{Cov}(XY)/\sigma_x^2]S = h^2S = [\text{Cov}(XY)/\sigma_x^2]i\sigma_x = [\text{Cov}(XY)/\sigma_x]i \quad [15]$$

where S is selection differential expressing the difference of the mean of selected individuals with the mean of the original population. From the standardized form, $S = i\sigma_x$, where i is the standardized selection differential called intensity of selection, and σ_x is the square root of phenotypic variance of the selection unit.

Model [15] assumes that phenotypic values of the trait studied are normally distributed and that selection has to be truncated. Based on this model the equation of expected selection response related to broad sense heritability is $R = (\sigma_G^2/\sigma_x^2)S = HS$, where H is broad sense heritability. Selection response expressed in terms of narrow sense heritability (Hallauer and Miranda, 1988) considers the parental control, as

$$R = (cr\sigma_A^2/\sigma_x^2)S = ch^2S \quad [16]$$

Where r is the coefficient for additive variance in the numerator related to a specific mating design, i.e., r is the coefficient of relationship (coancestry) between the offspring X in the evaluation stage and offspring Y in selection or predicted stage of the schemes given by Fehr (1987) and Nyquist (1991); while c is the parental control factor that is calculated as a ratio of the coefficient of additive variance in the numerator with the

coefficient of additive variance in the denominator and takes values of $\frac{1}{2}$, 1, or 2 to be used in calculating the selection response in heritability terms, i.e. eq. [16].

Equation [16] is valid for cross-fertilized crops and under the assumption of no epistatic interaction of any kind. It also assumes that the population of offspring evaluated is large enough, so that the genetic drift does not effect the precision of the response prediction parameter (Cockerham, 1963; Falconer, 1989).

Total response expected in the next generation is due to changes in allelic frequencies in the maternal set of genes from female parent (R_f), and that due to changes in allelic frequencies in the paternal set of genes from male parent (R_m), both having equal weights. Expected selection response is:

$$R = R_f + R_m = [\text{Cov}(X_f, Y)/\sigma_{xf}^2]i_f \sigma_{xf} + [\text{Cov}(X_m, Y)/\sigma_{xm}^2]i_m \sigma_{xm} \quad [17]$$

Since no sexual dimorphism exists in plants for most of the traits, both parts of eq.[17] are assumed equal and $\text{Cov}(X, Y) = 2 \text{Cov}(X_f, Y)$, and the expected selection response becomes:

$$R = 2 [\text{Cov}(X_f, Y)/\sigma_x^2]i\sigma_x = 2 [\text{Cov}(X_f, Y)/\sigma_x]i \quad [18]$$

If we refer to a half-sib remnant method (Nyquist, 1991), $\text{Cov}(X_f, Y) = 1/4\sigma_A^2$. By substituting this in eq. [18] we obtain $R = i1/2\sigma_A^2/\sigma_x$. Since $\sigma_x^2 = 1/4\sigma_A^2 + 1/4\sigma_{AL}^2 + \dots$, then $c = 2$ and the expected selection response in heritability terms would be $R = 2h^2i\sigma_x$.

Covariances for many different selection schemes of intra- and inter-population are given by Hallauer and Miranda (1988), under the assumption of no epistasis. Fehr (1987) and Nyquist (1991) provide procedures of expected selection response for many selection systems.

Eq. [18] can be used to estimate selection response for self fertilized crops by using the proper covariance, i.e., $\text{Cov}(X, Y/t; g, g')$ of a random individual Y in any generation $g' > g$ (Cockerham, 1983 ; Cockerham and Matzinger, 1985). The parental control is always 1.0 in self-fertilizing crops. Depending on the covariance used, next generation or long term gain can be predicted. The long term response of homozygous descendants without further selection from generation g , includes a covariance that does not have a dominance effect but that is not only function of σ^2_A because it includes epistatic interaction of additive by additive as well as other epistatic interactions (Cockerham and Matzinger, 1985). In the selection practice, these components are routinely neglected and very often the estimators of selection response are biased.

1.2 Response to Waterlogging

The primary effect of excess water (waterlogging) in soil is oxygen deficiency. Although roots are capable of respiring anaerobically, if this continues for some hours irregularities in metabolism occur. When partial pressure of oxygen drops to 1-5 Kpa, the soil environment is under hypoxia (Larcher, 1995). At this point root growth stops, and root tips entering the low-oxygen zones die. As soon as soil is oxygen-free, anaerobic microorganisms take over, creating a strongly reducing milieu in which Fe^{+2} , Mn^{+2} , H_2S , sulphides, lactic acid, and other substances are in toxic concentrations. Transformation of nitrogen in the soil is also impaired, mainly by a higher rate of denitrification (Drew, 1991; Bufogle et al., 1997).

In the event of hypoxia, respiration in the plant switches to anaerobic dissimilation, associated with aldehyde and ethanol accumulation. Absciscic acid and

ethylene are formed in large amounts causing partial stomatal closure and abscission (Bradford and Young, 1981). Cellular membrane systems break down, mitochondria and microbodies disintegrate and their enzymes are partially inhibited (Larcher, 1995).

1.2.1 Soil - Plant Relationship

Pore spaces in most well drained soils make up to 25% of their volume. When a soil becomes waterlogged, the rate of oxygen depletion depends on the respiration rate of roots and soil microorganisms, the solubility of oxygen in the water and the rate of oxygen diffusion through the soil to respiring roots (Barrett et al., 1988; Drew, 1991). The metabolism of roots and microorganisms consumes the remaining oxygen and produces carbon dioxide. Trought and Drew (1982), found that waterlogging eliminated gas filled pores and reduces gas exchange between soil and air within a few hours following flooding. Oxygen deficiency is considered to be the primary negative effect of waterlogging. Plants showed damage from oxygen depletion before any soil solutes attained injurious concentrations and while soil nitrate was still present (Trought and Drew, 1982).

Waterlogging affects nitrogen deficiency by stimulating denitrification and leaching (Armstrong and Webb, 1985; Trought and Drew, 1982; Hodgson et al., 1989; Sharma and Swarup, 1989; Huang et al., 1994; Buffogle et al., 1997). In waterlogged soils the nitrification process will be interrupted and the rate NH_4^+ to NO_2^- will increase as compared to NO_2^- to NO_3^- , which has the negative effect of the accumulation of NO_2^- that is toxic to plant roots (Brady, 1990). When soils become waterlogged, denitrification that is an anaerobic process will take place instead of nitrification that is an aerobic

process. Some anaerobic organisms have the ability to take their O_2 from NO_2^- or NO_3^- , with the accompanying release of N_2 or N_2O . Therefore, while the products of denitrification are being accumulated in the soil water, the nitrate concentration in the soil solution declines. The rate of this process depends on the soil temperature. The loss of nitrate is retarded in the cooler soils.

In anaerobic soils potentially inhibitory and toxic concentrations of carbon dioxide, ethylene, manganese, iron and organic substances may accumulate. Trought and Drew (1982) found carbon dioxide concentrations to increase linearly with time of waterlogging. Similar results were found by Armstrong and Webb (1985) and Ponamperuma (1984). Anaerobiosis of plant root system affects the synthesis of many hormones, such as abscissic acid and ethylene (Hiron and Wright, 1973; Trought and Drew, 1982; Larcher, 1995).

Waterlogging increased Fe and Mn concentration in the shoots of susceptible wheat varieties, leading to possible toxicity problems (Huang et al., 1994). In the waterlogged soils ferric and manganic forms are converted to the more reduced and soluble ferrous and manganate forms which are more readily taken up by roots.

1.2.2 Waterlogging Effects on Plants

Insufficient oxygen in plants results in anaerobic respiration and fermentation of carbohydrates into alcohol. The energy produced is not sufficient for the normal metabolism, which results in reduced shoot and root growth, dry matter accumulation and final yield (Kozlowski, 1984; Musgrave, 1994; Huang et al., 1995).

Waterlogging effects several physiological processes, such as absorption of water, photosynthesis, root and shoot hormone relations (Musgrave, 1994; Huang et al., 1995). In addition waterlogging effects include a decrease in uptake and transport of ions through roots causing nutrient deficiencies (Trought and Drew, 1980b; Hodgson et al., 1989; Huang et al., 1995).

Shortly after flooding plants respond with sequential changes in metabolism such as storing products of photosynthesis nearby the demanding sink, maintaining the glucose supply, adjusting carbon metabolism, adequately controlling glycolysis, maintaining the energy change and by retaining the integrity of membranes and organelles (Davies and Hillman, 1988; Waters et al., 1991). Wheat seedlings respond to oxygen deficiency by accumulating soluble carbohydrates in their roots and shoots (Trought and Drew, 1980b; Albrecht et al., 1994; Huang et al., 1995). Increased carbohydrate content of the foliage under waterlogging stress has been hypothesized to be related to the diminished metabolic sink activity of the root system (Musgrave, 1994; Larcher, 1995). Re-using the stored carbohydrates immediately after resuming aeration may be an adaptive way to reduce the oxygen concentration in the root zone. Leakage of H^+ from the vacuole to the cytoplasm due to oxygen deficit may cause cytoplasmic acidosis which reduces the survival time of plants under waterlogged conditions.

Carbon balance in roots is very sensitive to anoxia. It has been suggested that species sensitive to waterlogging suffer an acceleration of glycolysis and production of ethanol. Tolerant species switch from ethanol to malate production (Crawford, 1978).

Waterlogging effects on plants depend on a number of factors. They are markedly influenced by the growth stage of the crop. Gardner and Flood (1993) found that later maturing wheat genotypes yielded similarly with and without drainage whereas earlier genotypes yielded much less in undrained as compared to drained areas. Temperature can greatly modify the response of plants to waterlogging. In temperate climates the tolerance of waterlogging-susceptible species is generally greater during winter and cool springs than in warmer springs or summer temperatures (Trought and Drew, 1982).

The plant root system is one of the organs, most affected by waterlogging. Root weights of waterlogged plants have been found significantly lower than those of drained plants. Typical responses of the root mass of wheat to waterlogging are slower root growth, restriction of seminal, nodal and lateral root growth, and decreased nutrient accumulation. (Trought and Drew, 1982; Huang et al., 1994; Musgrave and Ding, 1998). In most plants continues root growth during waterlogging is feasible only when aerenchyma exists or develops (Armstrong and Webb, 1985; Waters et al., 1991, Larcher, 1995). Formation of aerenchyma was observed within five to seven days of waterlogging in wheat (Thompson et al., 1992). Waterlogging in wheat enhanced formation of aerenchyma in both seminal and nodal roots (Huang et al., 1995; Boru, 1996). Existence and continuity of aerenchyma in roots improves oxygen transportation from shoots to roots and root growth in anaerobic environments (Drew, 1991).

Waterlogging reduces plant growth and yield in several ways. In cereals, the main effects of waterlogging include reduced rate of leaf elongation and accumulation of

dry matter, premature senescence of leaves, decreased tillering, wilting, sterility and reduced kernel number and grain yield (Luxomore et al., 1973; Trought and Drew, 1982; Cannell et al., 1984; Kozlowski, 1984; Larcher, 1995). Gardner and Flood (1993) found a decrease in wheat yield as a result of fewer grains filling per ear under the influence of waterlogging. Cannell et al. (1984) found that winter waterlogging reduced tillering and ear number, resulting in 24% yield reduction. Besides reducing the number of fertile tillers, short-term waterlogging delayed ear emergence (Sharma and Swarup, 1989).

Waterlogging reduce the concentration of N, P, K, Ca, Mg and Zn in leaves and stems of wheat (Trought and Drew, 1982; Huang et al., 1995). This is most likely attributed to the inhibitory effects of waterlogging on ion uptake and transport mechanisms of roots (Trought and Drew, 1980b). This process could be due to the restriction of root growth (Pezeshki, 1994), and the inefficiency of anaerobic metabolism in providing adequate energy for active ion uptake (Trought and Drew, 1980b).

During waterlogging wheat plants translocate nitrogen from older to younger leaves, giving a typical yellowing and early senescence of the lower and older leaves. Boru (1996) found that percent chlorosis induced by waterlogging had a large direct effect on plant height, yield and kernel number, indicating that it can be used as a selection criteria for tolerant genotypes.

One possible mechanism for waterlogging to influence yield is through depressed photosynthetic rates. Huang et al. (1995) and Musgrave and Ding (1998) found that leaf photosynthetic rates in wheat declined during waterlogging stress.

1.2.3 Genetics of Waterlogging Tolerance

Breeding for waterlogging tolerance in wheat is a major objective given the severe problems of inadequate soil drainage in many areas of the world. There is some evidence of genetic variation for this trait in wheat. Davies and Hillman (1988) demonstrated variation in vegetative growth and yield under continuous flooding of four week old plants of various wheat species, with the hexaploid *Triticum macha* and the tetraploid *Triticum dicoccum* being the most tolerant. Van Ginkel et al. (1991) identified 14 waterlogging tolerant spring wheat lines by screening a large number of genotypes. Sayere et al. (1994) using a five week waterlogging stress identified six tolerant genotypes in terms of number of tillers, leaf chlorosis, senescence, fertility, grain yield and kernel weight.

The presence of a few genes in grasses for anoxic tolerance was suggested by Mujer et al. (1993). Testing intervarietal substitution lines in wheat seedlings for tolerance to seven days of flooding, Poysa (1984) found that the homologous group five chromosomes were associated with positive effects on seedling survival. Taeb et al. (1993) tested a number of Triticeae species for tiller production, shoot dry matter production and root penetration in waterlogged soil. Using these criteria they found *Thinopyrum elongatum* and *Elytrigia repens* to have better tolerance than wheat. The presence of chromosomes 2E and 4E of *Th. Elongatum* was associated with a positive effect on root growth in waterlogged conditions.

Boru (1996) studied the segregation ratios of all possible crosses between three waterlogging tolerant spring wheat lines and two sensitive cultivars. Segregating lines

were classified for waterlogging tolerance based on percentage chlorosis and chi-square was used to test the goodness of fit of the genetic model of segregation. In total four genes for waterlogging tolerance were estimated.

Although some progress is achieved in genetic studies identifying some of the genes responsible for waterlogging tolerance (Hart, 1980; Good and Crosby, 1989; Umeda and Uchimiya, 1994), no specific studies are reported on heritability of waterlogging tolerance. Most of the traits used as waterlogging selection criteria are quantitative and highly influenced by environmental factors. Their genetic control is confounded by environmental stress. By studying the heritability of the traits influenced the most by waterlogging it is possible to account for heritable and non-heritable factors influencing waterlogging tolerance, and evaluate traits as selection indicators.

2. LOSSES DUE TO WATERLOGGING

2.1 Introduction

Wheat along the Gulf Coast and many other regions is frequently subjected to waterlogging due to heavy rainfall, level topography, and inadequate soil drainage. In Louisiana, waterlogging is one of the factors depressing wheat yield especially when it occurs in the first months of growth (Musgrave, 1994). A watertable at, or close to the soil surface has been shown to reduce grain yield of winter wheat by about 20% (Belford, 1981, Cannell et al., 1984). More recently Musgrave and Ding (1998) have estimated yield losses in wheat of 40 to 50% in waterlogged as compared to well-drained soil. Boyer (1982) estimated that 12% of agricultural soils in the USA are affected by waterlogging.

Oxygen deficiency caused by waterlogging reduces shoot and root growth, dry matter accumulation and final yield by depressing absorption of water (Trought and Drew, 1980a)), reducing photosynthesis (Huang et al, 1994; Musgrave, 1994), leaching of nutrients (Armstrong, 1985; Hodgson et al., 1989) and accumulation of toxic substances (Ponamperuma, 1984; Huang et al., 1994).

Waterlogging affects several physiological processes, such as absorption of water (Drew, 1991), root and shoot hormone relations (Huang et al., 1994) and photosynthesis (Musgrave, 1994; Huang et al., 1995). Waterlogging also decreases uptake and transport of ions through roots causing nutrient deficiencies (Trought and Drew, 1980b; Hodgson et al., 1989; Huang et al., 1995). In cereals, waterlogging reduces leaf elongation, decreases tillering and kernel number (Luxomore et al., 1973; Trought and Drew, 1982)

In the absence of direct and reliable selection markers for waterlogging tolerance, a successful breeding program in wheat requires the identification of the physiological or morphological traits influenced the most by waterlogging and the existence of enough genetic variability controlling their expression. There is some evidence of genotypic differences in tolerance to waterlogging in wheat. Davies and Hillman (1988) demonstrated variation in vegetative growth and yield under continuous flooding of various wheat species. Van Ginkel et al. (1991) screened a large number of genotypes and identified 14 waterlogging tolerant spring wheat lines. In further studies Sayer et al. (1994), using a five week waterlogging treatment, identified six tolerant genotypes in terms of number of tillers, leaf chlorosis, senescence, fertility, grain yield and kernel weight. Other varietal studies for waterlogging stress in wheat have been reported (Thomson et al., 1992; Musgrave and Ding, 1998). Some initial progress has been achieved in genetic studies identifying genes responsible for waterlogging tolerance (Mujer et al., 1993; Waters et al., 1991; Taeb et al., 1993; Umeda and Uchimiya, 1994).

Most of the traits used to evaluate waterlogging tolerance are quantitative, i.e., morphological or physiological. Losses caused by waterlogging need to be measured in order to determine the importance of traits used as waterlogging tolerance indicators.

The objective of this study was to determine the response to different levels of waterlogging of several quantitative traits, including yield, in a rain shelter conditions; and to estimate losses from waterlogging in a field experiment. Both studies identify traits to be used as selection criteria and in quantifying losses from waterlogging that can be expressed in economic values, useful in breeding for waterlogging tolerance in wheat.

2.2 Materials and Methods

Two experiments were conducted. The first experiment was conducted in rain shelter to avoid the influence of rainfall on waterlogged treatment. The aim of this experiment was to evaluate the response of yield and other traits to different levels of waterlogging. The experiment was started in the greenhouse for the first four weeks and then transferred to the shelter. The second experiment was conducted in the field. The objective of this experiment was to evaluate losses from waterlogging, by comparing the flooded treatment with the control, and to screen some of the main genotypes of the wheat breeding program for their tolerance to waterlogging.

2.2.1 Shelter Experiment

Genotypes studied in this experiment were: 1) Pioneer 2643, 2) Pioneer 2691, 3) LA 87167, 4) Savannah, 5) Terral LA 422, 6) Coker 9663, 7) Tchere, 8) Florida 304, 9) FFR502W, and 10) Jaypee. In general, they represent soft red winter wheat genotypes that are important parental components in wheat breeding programs and have shown good performance in wheat trials (Harrison et al., 1997). More specifically, Tchere is known to be waterlogging tolerant but very susceptible to disease, especially to leaf rust, caused by *Puccinia triticina* Eriks, while Terral LA 422 is a cultivar released by the Louisiana Agricultural Experiment Station (LAES).

Seeds from each genotype were planted in a polyvinylchloride (SC-10) cone-tainer (25cm long by 10cm diameter) containing 0.55 kg of comeced silt loam soil taken from the LAES Central Station Ben Hur Research Farm of Louisiana State University at Baton Rouge. An equivalent amount of 90 kg N ha⁻¹ urea was added to the

soil of each cone-tainer. The cone-tainers were held in plastic holders inside a plastic tank (140cm L x 50cm W x 30 cm H). After germination seedlings were thinned to one plant per cone-tainer. The plants were grown in the greenhouse until one week before starting the waterlogging treatment. After that the experiment was transferred to a rain shelter, under controlled rainfall, but in similar weather conditions as the field experiment. Plants were allowed to acclimate one week before starting the waterlogging treatment.

The waterlogging treatment was initiated about five weeks after seeding. Depending on the genotype this period coincided with 3-5 leaf stage. Waterlogging was accomplished by raising the level of water in the tanks to the surface of the PVC containers, so that the top soil was wet during the time of treatment. Four periods of waterlogging were applied: none, 10 days, 20 days, and 30 days (Fig. 2.1). Each period (treatment) of waterlogging was followed by a two day period of completely drained tanks, in order to apply the equivalent of 30 kg ha⁻¹ N fertilizer as urea.

The experimental design was a split-plot design: CRD-RCBD with three replications (Hinkelman and Kempthorne, 1994). Each waterlogging level was randomly assigned to three of the 12 tanks, creating the main plots, while wheat genotypes were randomly assigned to one cone-tainer per tank each, creating the sub-plots.

During 1997-98 and 1998-99, measurements for each plant were taken for chlorophyll content, tillers plant⁻¹, height, kernels head⁻¹, and yield. Measurements on chlorophyll content were taken four times corresponding to the four waterlogging periods, starting right before applying waterlogging and at 10 day intervals.

Figure 2.1. Shelter experiment to study the effect of different waterlogging treatments in soft red winter wheat, at the Ben Hur Research Farm Station, in Baton Rouge, 1999.

Three to four readings were taken for each measurement and the mean was used for the data analysis. A spad meter was used to take measurements for chlorophyll content. Since several measurements were made over time on the same plants, data collected on chlorophyll content were analyzed according to repeated measures design.

2.2.2 Field Experiment

Wheat cultivars and lines included in this experiment were: 1) Pioneer 2643, 2) Shelby, 3) Pioneer 2691, 4) LA 87167, 5) Savannah, 6) AR-584A-3-2, 7) Terral LA422, 8) Coker 9663, 9) Mason, 10) Pioneer 2684, 11) Pioneer 26R61, 12) Florida 304, 13) FFR 502W, 14) Jaypee, and 15) GA 871339. The waterlogging treatments were none (control) and five weeks of continuous flooding, starting at the 4-6 leaf stage. The experimental design was a split-plot with three replications, with waterlogging treatments in the main plots and genotypes in the subplots. Plots consisted

of six rows 1 m long and 20 cm apart. Soil type was a Commerce silt loam (fine silty, mixed, nonacid, thermic Aeric Fluvaquent). Pre-plant fertilizer at a rate of 240 kg ha⁻¹ of N-P-K and Glean (clorsulfuron) herbicide at 53 ga.i. ha⁻¹ were applied. Levees were constructed for each main plot with a height of 30-40 cm. Waterlogging was accomplished by pumping water from a ditch and flooding the plots with the waterlogged treatment. The soil was kept saturated by continuous flooding, usually every day for each waterlogged plot. A top dressing of 90 kg-ha⁻¹ N as ammonium nitrate was applied immediately after the period of waterlogging treatment ended.

Soil oxygen content was measured using gas samplers constructed of porous sintered bronze cups attached to sampling taps (Musgrave and Ding, 1988). After seedling emerged, gas samplers were buried in the soil between rows at a depth of 10 cm in every main plot. Measurements on redox potential were taken weekly, beginning one week prior waterlogging treatment and ending one week after termination of waterlogging. Gas samples of 20 ml were withdrawn through the sampling taps with a 50 ml syringe. Oxygen concentration of the samples was determined by using an oxygen probe (DO-166, Lazar Research Laboratories, Los Angeles, CA).

Data were taken on chlorophyll content, height, number of tillers, kernels head⁻¹, kernel weight and yield. Chlorophyll content measurements were taken on three plants per plot, immediately after the waterlogging period. Height from the soil surface to the base of the head (in cm), was measured on three random plants per plot. Plot means were used for data analysis of chlorophyll content and height. Tiller number was measured before harvest, by counting the number of heads in 20 cm of an interior row in each plot

Figure 2.2. Flooded (left) and control plot (right) in a split-plot design experiment to study losses from waterlogging in wheat, conducted in 1999-2000, at the Ben Hur Research Farm, in Baton Rouge.

and then converted to tiller number m^{-2} . Kernels head^{-1} were measured on three random heads per plot and the mean was used in data analysis. Kernel weight was determined from a 100 seed sample from each plot. Yield in kg ha^{-1} was measured by hand harvesting and threshing two rows per plot. This experiment was conducted for three years: 1997-98, 1998-99, and 1999-00, at Central Station Ben Hur Research Farm, Baton Rouge.

2.2.3 Statistical Analysis

In the shelter experiment, the times of taking measurements on chlorophyll content every 10 days were analyzed as repeated measures, according to the univariate model:

$$y_{ijl} = \mu + w_i + \gamma_{il} + m_j + (wm)_{ij} + \epsilon_{ijl} \quad [19]$$

where μ is the overall mean effect, w_i is the waterlogging treatment effect, γ_{il} is the random effect for the l th genotype, m_j is the effect of measurement ($j=1$ to $j=4$ measurements), $(wm)_{ij}$ is the interaction effect of the i th treatment with the j th measurement, and ϵ_{ijl} is the random error among measurements across the plants. For hypothesis testing, it is assumed that ϵ_{ijl} is normally distributed with mean zero, variance σ^2 , and covariance:

$$\text{cov}(\epsilon_{ijl}, \epsilon'_{ijl}) = \sigma^2 \begin{pmatrix} 1 & \rho & \rho & \rho \\ \rho & 1 & \rho & \rho \\ \rho & \rho & 1 & \rho \\ \rho & \rho & \rho & 1 \end{pmatrix}$$

where ρ is the correlation among errors and ϵ'_{ijl} is the vector of four repeated measures errors on the l th plant. This covariance structure satisfies the sphericity requirement of the univariate approach to repeated measures (Huynh and Feldt, 1970).

A univariate model was used to study the trend response of chlorophyll content to waterlogging treatments for the linear, quadratic, and cubic component. Data were unbalanced and the analyses were performed in PROC MIXED of SAS, v.6.12.

Data for other traits were analyzed according to a split-plot design (Steel and Torrie, 1981; Hinkelmann and Kempthorne, 1994), with waterlogging treatment in the main plot and genotypes as subplots. Since the duration of the waterlogging treatments were equidistant (10 days), a trend analysis was performed to determine if the response of traits to waterlogging was linear, quadratic or cubic. Trend analysis was based on orthogonal polynomials (Hinkelmann and Kempthorne, 1994).

Data of experiment in the field were analyzed as a split-plot design according to the model:

$$y_{ijk} = \mu + r_i + \alpha_j + e_{ij} + \beta_k + (\alpha\beta)_{jk} + e_{ijk} \quad [20]$$

where r_i is the effect of the i th replication, α_j is the effect of the j th level of waterlogging, β_k is the effect of the k th genotype, and $(\alpha\beta)_{jk}$ is the effect of their interaction, e_{ij} and e_{ijk} are the random errors for waterlogging treatment and genotypes, respectively. Multiple comparisons were performed to screen genotypes for their tolerance to waterlogging. Data for this experiment were balanced. The analysis were performed in PROC GLM of SAS, v.6.12.

2.3 Results and Discussion

2.3.1 Trend Response to Waterlogging

The average chlorophyll content of all genotypes decreased with time for both years of study (Table 2.1). The univariate corrections using Greenhouse-Geisser and Huynh-Feldt gave the same probability values, suggesting that the univariate model was a good approach for the repeated measures data (Moser et al., 1991). Duration of waterlogging from 0 to 30 days had a significant effect on the average chlorophyll content of

all genotypes. There was a significant linear reduction in chlorophyll content with longer period of waterlogging, for both years of study (Table 2.1). Although the quadratic component was significant for the first year, and the cubic component was significant for the second year of study, they are not as much important as the linear trend. P values for quadratic and cubic are much smaller than P values for the linear trend. Decrease in chlorophyll content as a result of waterlogging reduces photosynthesis in wheat with a significant effect in yield (Drew, 1991). Significant reduction in chlorophyll content from waterlogging has been previously reported (Huang et al., 1994).

A significant interaction of time by treatment for both years of the study indicated that the average chlorophyll content of all genotypes with time changed among the four levels of waterlogging treatment. This means that the difference in chlorophyll content between two subsequent times for a given level of waterlogging is not the same with the difference in chlorophyll content between the same times for another level of waterlogging. The four profiles corresponding to four levels of waterlogging are not parallel in time, and a comparison of waterlogging main effect is not meaningful for chlorophyll content. Time by genotype interaction was significant (Table 2.1), indicating that the average chlorophyll content based on four waterlogging treatments changed in time for individual genotypes. Therefore, comparison of mean chlorophyll content of genotypes needs to be done for a specific time rather than averaging the measurements over time.

A significant linear and quadratic response to waterlogging was observed for yield, a significant linear response was observed for kernels head⁻¹, and tiller plant⁻¹, and

Table 2.1. Univariate repeated measures analysis for chlorophyll content of nine wheat genotypes under four levels of waterlogging treatment studied in a split plot experiment in 1998 and 1999 under rain shelter.

Source of Variation	df	SS		F		P > F		Adj. P > F			
		1998	1999	1998	1999	1998	1999	G-G		H-F	
								1998	1999	1998	1999
Waterlogging (WLogg.)	3	8698.8	4447.4	136.1	46.2	0.0001	0.0001				
Linear	1	8572.2	4249.1	402.2	132.3	0.0001	0.0001				
Quadratic	1	127.1	0	5.9	0	0.0178	0.9642				
Cubic	1	40.2	198.3	1.9	6.2	0.1739	0.0153				
Genotypes (Gen.)	8	1872.4	2790.2	10.9	10.9	0.0001	0.0001				
Wlogg x Gen.	24	392.2	490.8	0.8	0.6	0.7472	0.8921				
Measurements (Mst.)	3	4843.4	4929.9	120.3	132.0	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
Mst. x WLogg.	9	7716.1	3033.2	63.9	27.0	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
Mst. x Gen.	24	629.9	465.9	1.9	1.6	0.0067	0.0520	0.0152	0.0826	0.0067	0.0520
Mst. x Wlogg. x Gen.	72	888.5	646.4	0.9	0.7	0.6544	0.9469	0.6312	0.9098	0.6544	0.9469
Error	69	1470.6	2312.1								

Adj. P > F are probabilities associated with the Greenhouse-Geisser (G-G) and Huynh-Feldt (H-F) adjusted F-test

a significant linear and cubic response was observed for height (Table 2.2). The linear component was the most important component, explaining most of the variability due to waterlogging treatment. Expressed in percentage of treatment sum of square, the linear component was 95% for yield, 99% for kernels head⁻¹, 99% for tillers plant⁻¹, and 92% for height (Table 2.2).

A regression analysis was performed to test which of the models best described the trend of response to the four levels of waterlogging (Table 2.3). Three models of regression: linear, quadratic, and cubic were constructed for each trait and then the parameters were tested. For the linear regression both parameters, intercept and regression coefficient were significantly different from zero for all the traits. Although values of regression coefficients significantly different from zero were observed in the quadratic model for yield, kernels head⁻¹, tillers plant⁻¹, and height, a 'lack of fit test', classified the quadratic model as inappropriate. The cubic model had values of regression coefficients different from zero for height, but was also an inappropriate model as indicated by the lack of fit test.

In summary, the trend response of wheat genotypes to 0, 10, 20 and 30 days of waterlogging treatments can be considered as a linear reduction in yield, kernels head⁻¹, tillers plant⁻¹, and height. Linear regression lines in Figures 2.3, 2.4, 2.5, and 2.6 were constructed based on the parameters obtained for the linear model in Table 2.3. Yield and tillers plant⁻¹ were the traits influenced the most by waterlogging. They had the sharpest reduction resulting from waterlogging. According to the linear model, $y = 3.09 - 0.06X$ (Fig. 2.3), yield is expected to decrease at about 60%, from 3.09 g plant⁻¹ for the

Table 2.2. Split-plot trend analysis for yield, kernels/head, tillers/plant, and height of nine wheat genotypes grown under four levels of waterlogging in 1998 and 1999 in a rain-shelter experiment.

Source of variation	df	Yield (gr.)†	Kernels/head	Tillers/plant	Height (cm)
Replication - Rep	2	0.75	44.91	0.52	0.39
Waterlogging treatment - W.logg.TRT	3	54.78**	1204.22**	51.89**	1347.97**
Linear	1	51.99 (95%)**‡	1191.12 (99%)**	51.03 (98.5%)**	1231.07 (92%)**
Quadratic	1	2.10 (4%)*	0.04 (0%)ns	0.59 (1%)ns	2.15 (1%)ns
Cubic	1	0.69 (1%)ns	13.06 (1%)ns	0.27 (0.5%)ns	114.74 (8%)*
Rep x W.logg.TRT	6	0.17	40.05	1.55	24.34
Genotypes	8	17.73**	584.35**	21.68**	1153.43**
W.logg.TRT x Genotypes	24	13.57**	664.61**	6.61	670.58**
Error	64	1.19	101.70	13.26	105.37

† Column of each trait indicates sum of squares.

‡ Value in bracket is percentage of waterlogging treatment sum of squares explained by the linear component.

*,** significant at the 0.05 and 0.01 probability level.

ns = non significant.

Table 2.3. Polynomial regression to evaluate the relationship among levels of waterlogging and yield, kernels/head, tillers/plant, and height of nine wheat genotypes in a rain shelter experiment.

Regression model	Yield		Kernels/head		Tillers/plant		Height	
	Parameter value	Probability for $H_0: \text{Parameter}=0$	Parameter value	Probability for $H_0: \text{Parameter}=0$	Parameter value	Probability for $H_0: \text{Parameter}=0$	Parameter value	Probability for $H_0: \text{Parameter}=0$
<u>Linear</u>								
Intercept ($\hat{\beta}_0$)	3.098	0.0001	30.4185	0.0001	3.7185	0.0001	48.1094	0.0001
Treatment ($\hat{\beta}_1$)	-0.062	0.0001	-0.2970	0.0001	-0.0614	0.0001	-0.3019	0.0001
<u>Quadratic</u>								
$\hat{\beta}_0$	2.959	0.0001	30.4000	0.0001	3.6444	0.0001	48.2506	0.0001
$\hat{\beta}_1$	-0.020	0.2407	-0.2914	0.0105	-0.0392	0.0464	-0.3443	0.0114
$\hat{\beta}_1^2$	-0.001	0.0125	-0.0002	0.9588	-0.0007	0.2365	0.0014	0.7418
F test of 'lack of fit'	47.4**		16.1**		3.57**		29.1**	
<u>Cubic</u>								
$\hat{\beta}_0$	2.9948	0.0001	30.5555	0.0001	3.6666	0.0001	47.7896	0.0001
$\hat{\beta}_1$	-0.0762	0.0715	-0.5352	0.0538	-0.0741	0.1245	0.3778	0.2405
$\hat{\beta}_1^2$	0.0039	0.2864	0.0231	0.3420	0.0026	0.5410	-0.0677	0.0184
$\hat{\beta}_1^3$	-0.0001	0.1461	-0.0005	0.3328	-0.0001	0.4271	0.0015	0.0151
F test of 'lack of fit'	44.7**		20.9**		3.79**		28.0**	

** , significant at the 0.01 probability level.

control to 1.2 g plant⁻¹ for the 30 days of waterlogging, while tillers plant⁻¹, $y = 3.72 - 0.061X$ (Fig.2.5) is expected to decrease by about 50%, from 3.72 tillers plant⁻¹ for the control to 1.92 tillers plant⁻¹ for the 30 days of waterlogging treatment. Kernels head⁻¹ and height had a less severe reduction. A decrease of about 30%, from 30.4 for the control to 21.2 for 30 days of waterlogging treatment, is expected for kernels head⁻¹, while height, $y = 48.1 - 0.3X$, is expected to decrease at about 19%, from 48.1 cm for the control to 39 cm for the 30 days of waterlogging treatment (Figure 2.6). Musgrave and Ding (1998) reported similar grain yield decrease in wheat genotypes grown under waterlogging treatments in rainshelter conditions. They determined that kernel number was the main factor responsible for yield reduction. In this study, the reduction in yield is largely due to number of tillers per plant and to the number of kernels per head.

The usefulness of prediction equations for losses from waterlogging is to accurately describe the relationship between the measured traits and waterlogging levels. In previous studies (Musgrave and Ding, 1998) a linear relationship is presumed. The results of this study show that this is not always the case and different models need to be tested before measuring losses. Extreme limits of waterlogging stress ranging from 0 to 30 days, contribute to model estimation with a wide range in prediction.

The shelter experiment provided an environment to study the effect of different levels of waterlogging treatment and to estimate the model that best fits the response of yield and other traits. However this type of experiment has size limitations. Differences in the sample size and overall conditions in a controlled rainshelter as compared to a field experiment may result. Musgrave and Ding (1998) found that yield components responded somewhat differently in the greenhouse than in the field conditions.

Figure 2.3. Relationship between yield and four levels of waterlogging treatment of nine wheat genotypes grown in a rain shelter experiment.

Figure 2.4. Relationship between kernels/head and four levels of waterlogging treatment of nine wheat genotypes grown in a rain shelter experiment

Figure 2.5. Relationship between tillers/plant and four levels of waterlogging treatment of nine wheat genotypes grown in a rain shelter experiment.

Figure 2.6. Relationship between height of plant and four levels of waterlogging treatment of nine wheat genotypes grown in a rain shelter experiment.

2.3.2 Losses Due to Waterlogging

An alternative approach was used to estimate losses in yield in field conditions. Redox potential ranged from 290 to 337mV for the flooded plots, showing a high waterlogging stress, as compared to the control, ranging from 548 to 617 mV (Table2.4).

Table 2.4. Redox potential data from five weeks of waterlogging of 15 wheat genotypes in the field experiment, at the Ben Hur Research Farm, Baton Rouge.

Period	Redox potential (mV)								
	1997-98			1998-99			1999-00		
	Rep 1	Rep 2	Rep 3	Rep 1	Rep 2	Rep 3	Rep 1	Rep 2	Rep 3
Week 1 †	318	308	296	314	308	290	337	313	316
‡	595	605	613	591	600	610	595	605	603
Week 2 †	296	307	306	295	300	313	306	307	302
‡	601	611	617	600	616	608	609	611	612
Week 3 †	305	315	325	300	315	320	305	323	314
‡	598	608	604	590	600	601	588	590	604
Week 4 †	334	314	317	333	310	307	324	314	301
‡	548	588	573	578	608	570	567	578	593
Week 5 †	318	306	329	308	300	317	306	302	318
‡	617	617	611	580	594	604	593	587	602

† data from flooded plots.

‡ data from control plots.

Significant effects for waterlogging treatment were observed on all traits. (Table 2.5). A decrease of 44% was observed for yield (Fig. 2.7). Sharma and Swarup (1989), observed a 39% reduction, while Musgrave and Ding (1998) found a 45% decrease in wheat yield. They and others (Gardner and Flood, 1993), identified number of kernels as the primary factor responsible for yield losses. In this study, yield losses are due mainly to a combined effect of reduced tiller and kernel number.

Table 2.5. Split-plot ANOVA for yield, chlorophyll content, height, kernels/head, kernel weight, and tiller number of 15 soft red winter wheat genotypes grown under waterlogging treatment in a field experiment in 1997-2000.

Source of variation	df	Yield †	Chlorophyll	Height	Kernels/head	Kernel weight	Tiller number
Year	2	137.5**	361.3**	12057.9**	1668.4**	0.06	
Waterlogging treatment - TRT	1	247.1**	3978.1**	5432.1**	2960.5**	3.83**	11042717**
Genotypes - GEN	14	29.9**	60.5**	366.3**	125.4**	2.21*	256378**
Rep(Year)	5	0.3	25.3	47.1	11.1	0.06	168051
TRT x Rep(Year)	5	0.2	9.2	23.3	3.4	0.03	13896
TRT x GEN	14	2.5**	8.1	56.8**	36.4**	0.07*	116008**
TRT x Year	2	19.9**	71.4**	99.5**	393.1**	1.00**	
GEN x Year	28	1.4**	16.5**	64.1**	54.8**	0.08**	
TRT x GEN x Year	28	0.9	6.0	21.9	29.6**	0.03	
Error	140	0.2	32.7	11.1	5.3	0.03	57551
R ² (%)		96	88	96	93	91	89
CV (%)		12	6	4	6	5	14

† Column of each trait indicates mean squares.

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

Figure 2.7. Response to waterlogging for yield, chlorophyll content, height, kernels/head, kernel weight, and tiller number of 15 wheat genotypes.

Figure 2.8. Yield response to waterlogging of Pioneer 2691, Terral LA 422, Coker 9663, AR-584A, and FFR 502W.

Tiller number was reduced by waterlogging more than other yield components, about 43% (Fig. 2.7). It had the strongest correlation with yield in control conditions, $r = 0.69$ (Table 2.6). Due to a higher influence of waterlogging stress on this trait as compared to the other traits, this association was less expressed, but still significant ($r = 0.24^*$, Table 2.6). The association of tiller number with other yield components were

Table 2.6. Phenotypic correlations among yield, and yield components, estimated in 15 wheat genotypes grown in control and under waterlogging stress.

Trait	Height	Tiller m ⁻²	Kernels head ⁻¹	Kernel weight	Yield
Chlorophyl	0.28**†	0.06	0.21*	0.10	0.33**
	0.42**‡	0.01	0.30**	0.46**	0.22*
Height		0.37**	0.25*	0.15	0.64**
		0.05	0.65**	0.32**	0.64**
Tiller m ⁻²			0.10	0.19	0.69**
			0.14	0.23	0.24*
Kernels head ⁻¹				0.13	0.27**
				- 0.1	0.54**
Kernel weight					0.44**
					0.30**

†) Values up each element of the matrix are correlation coefficients estimated in control conditions.

‡) Values down each element of the matrix are correlation coefficients estimated in w.logg. conditions.

*, **, significant at 0.05 and 0.01 probability level, respectively.

non-significant, suggesting that this trait has a direct influence on yield reduction as result of waterlogging stress. Kernel number was reduced about 21% (Fig. 2.7), and its correlation with yield was high, especially under waterlogging conditions ($r = 0.54^{**}$). Tiller and kernel number are the primary traits responsible for yield losses from waterlogging. They are easy to measure, and they can be used to test a large number of genotypes for waterlogging tolerance, especially in the early stages of breeding programs. Kernel weight and chlorophyl had a smaller influence on yield losses.

Correlations among yield and these traits were smaller than correlation of yield with tiller and kernel number under waterlogging conditions (Table 2.6) and the reduction was less severe than for other traits. Chlorophyll content decreased by 19%, and kernel weight decreased by 8%, as a result of waterlogging treatment.

Large yield losses observed in this study are a result of waterlogging stress in relation to the specific weather conditions of Louisiana, especially of high temperatures. Luxomore et al. (1973), found that yield of a semi-dwarf spring wheat was reduced by 15 to 23% in soils at 15-17° C, and by 73% in soils at 25° C. Trought and Drew (1982) found that wheat plants grown under waterlogging conditions at 10° C reached the same growth stage as those at 14° C, four days later. Low temperatures slow the rate of depletion of oxygen from the soil water by roots and soil micro-organisms. Root metabolism and that of other organs of plants is slowed by low temperatures, reducing the biological demand for oxygen.

2.3.3 Screening of Wheat Genotypes for Waterlogging Tolerance

Significant variability was observed among genotypes for their response to waterlogging for each of the traits, indicating the potential to identify tolerant genotypes. For yield, the 15 wheat genotypes were classified into four significantly different groups (Table 2.7). Despite the yield reduction observed in this experiment, some genotypes such as Terral LA 422 (4670 kg ha⁻¹), showed tolerance to waterlogging. The performance of this cultivar under waterlogging conditions was probably due to its ability to maintain a high number of kernels per head and a high number of tillers. Terral LA 422 was ranked among the best genotypes for kernel (37.8^{AB}) and tiller number (25^{AB}). Other tolerant genotypes under waterlogging stress, were Shelby (4440 kg ha⁻¹),

Table 2.7. Mean of 15 wheat genotypes for yield, chlorophyll content, height, kernel weight, kernels/head, and tiller number, from a field experiment under waterlogging.

Genotypes	Yield (kg ha ⁻¹)	Chlorophyll (%)	Height (cm)	Kernel (kernel/head)	Kernel wt. (g)	Tiller (tillers m ⁻²)
Pioneer 2643	3080 ^D	39.8 ^{BCDEF}	64.7 ^G	38.3 ^{AB}	3.10 ^I	990 ^{BC}
Shelby	4440 ^{AB}	41.2 ^{ABCD}	78.9 ^{AB}	39.2 ^A	3.71 ^{CDEF}	1228 ^{BC}
Pioneer 2691	4010 ^{BC}	40.8 ^{ABCDE}	71.7 ^{DEF}	29.9 ^F	3.99 ^B	1503 ^{AB}
LA 87167	3830 ^C	41.7 ^{ABCD}	70.8 ^F	37.4 ^{AB}	3.65 ^{DEFG}	1420 ^{AB}
Savannah	3880 ^{BC}	39.3 ^{BCDEF}	74.9 ^{CDE}	32.4 ^{DEF}	3.52 ^{EFGH}	1375 ^{AB}
AR-584A-3-2	2710 ^D	37.5 ^{FG}	72.8 ^{DEF}	33.9 ^{CDE}	3.37 ^H	861 ^C
Terral LA 422	4670 ^A	39.0 ^{CDEFG}	75.2 ^{BCD}	37.8 ^{AB}	3.41 ^{GH}	1375 ^{AB}
Coker 9663	4090 ^{ABC}	37.9 ^{EFG}	82.7 ^A	31.3 ^{EF}	3.78 ^{BCDE}	1329 ^{AB}
Mason	4220 ^{ABC}	41.8 ^{ABCD}	80.3 ^A	33.1 ^{CDEF}	3.93 ^{BC}	1475 ^{AB}
Pioneer 2684	4150 ^{ABC}	42.1 ^{ABC}	72.4 ^{DEF}	30.7 ^{EF}	3.88 ^{BCD}	1393 ^{AB}
Pioneer 26R61	4290 ^{ABC}	43.2 ^A	81.0 ^A	35.3 ^{BCD}	4.46 ^A	1145 ^{BC}
Florida 304	4070 ^{BC}	38.9 ^{DEFG}	78.7 ^{ABC}	38.8 ^A	3.95 ^{BC}	1246 ^B
FFR 502W	3770 ^C	42.3 ^{AB}	69.2 ^F	30.8 ^{EF}	3.51 ^{F GH}	1246 ^B
Jaypee	4000 ^{BC}	39.5 ^{BCDEF}	75.7 ^{BCD}	32.9 ^{DEF}	2.96 ^I	1650 ^A
GA 871339	2840 ^D	36.1 ^G	71.1 ^{EF}	36.3 ^{ABC}	2.84 ^I	1145 ^{BC}
Critical value	58	3.09	4.05	3.26	0.26	379

† Tukey's Studentized Range Test.

‡ Means with different letters are significantly different at p=0.05.

Pioneer 26R61 (4290 kg ha⁻¹), Mason (4220 kg ha⁻¹), Pioneer 2684 (4150 kg ha⁻¹), and Coker 9663 (4090 kg ha⁻¹). Genotypes such as AR-584A-3-2 (2710 kg ha⁻¹), GA 871339 (2840 kg ha⁻¹), belong to the group of genotypes with the lowest yield performance.

When screening for tolerant genotypes, it is important to check and interpret their interaction with waterlogging treatments. In this study, the interaction of genotypes with waterlogging treatment was significant for yield, and for some of the yield components, such as tiller number, kernels head⁻¹ and kernel weight (Table 2.5), showing that differences for the two levels of treatment (control and waterlogging) varied by genotypes. In terms of tolerance to waterlogging, the most tolerant genotypes are those with the smallest magnitude of interaction with waterlogging treatment. The reduction in yield of Coker 9663 or FFR 502W, from control to waterlogging level, is larger than the reduction in yield of Terral LA 422 or Pioneer 2691. This is due to a higher interaction of Coker 9663 and FFR 502W with waterlogging treatment. Genotypes such as Terral LA 422, which interact with waterlogging treatment, maintaining a high performance, would be desirable (Fig. 2.8). Genotypes with less interaction with waterlogging treatment, such as AR-584A, have a small reduction as a result of waterlogging.

The difference in yield between control and waterlogging were significant for all genotypes, except AR-584A. Nevertheless, those differences were not the same, showing different degree of tolerance at different levels of performance among genotypes (Fig. 2.9). Genotypes such as Terral LA 422, Shelby, Pioneer 2691, and Pioneer 2684 can be considered as the most waterlogging tolerant. They have a small reduction from

Figure 2.9. Mean yield response to waterlogging treatment of 15 wheat genotypes grown in 1997-2000, in a field experiment at the Ben Hur Research Farm, in Baton Rouge.

waterlogging, and high levels of yield performance. Some genotypes, such as Coker 9663, Mason, and, FFR 502W that have high mean yield in the absence of waterlogging (Fig. 2.9), show the largest reduction under waterlogging treatment. Although these genotypes might be a good choice for normal growing conditions, their placement in environments with expected waterlogging conditions would not be safe. Genotypes AR 584A and GA 871339 have the smallest decrease from waterlogging (Fig. 2.9), but their tolerance is demonstrated at the lowest yield performance levels. These genotypes might be with interest for introgression of waterlogging tolerance into breeding populations.

The results of screening demonstrate the importance of developing waterlogging tolerant cultivars for areas with excess soil water. Some of the most tolerant genotypes are advanced generation lines from wheat breeding programs in Louisiana (Harrison, et al., 1997), while the others are genotypes intensively used for crosses in wheat breeding. The potential of waterlogging tolerance found in some genotypes is important for identifying cultivars for specific areas, and for further utilization in wheat breeding programs.

3. HERITABILITY OF WATERLOGGING TOLERANCE

3.1 Introduction

Wheat (*Triticum aestivum* L.) along the Gulf Coast and many other regions is frequently subjected to waterlogging due to heavy rainfall, level topography, and inadequate soil drainage. In Louisiana, waterlogging is one of the factors depressing wheat yield, especially when it occurs in the first months of growth (Musgrave and Ding, 1998). It has been estimated that about 12% of agricultural soils in the U.S.A. are affected by excess soil water (Boyer, 1982).

There is some evidence of genotypic variation for tolerance to waterlogging in wheat. Davies and Hillman (1988) demonstrated variation in vegetative growth and yield under continuous flooding of various wheat species. Van Ginkel et al. (1991) identified 14 waterlogging tolerant spring wheat lines by screening a large number of genotypes. Sayre et al. (1994) using a five week waterlogging treatment identified six tolerant genotypes in terms of number of tillers, leaf chlorosis, senescence, fertility, grain yield and kernel weight. Other varietal studies for waterlogging in wheat have been reported by Thompson et al. (1992), Huang et al. (1994), and Musgrave and Ding (1998).

The presence of a few genes in grasses for hypoxia tolerance was suggested by Mujer et al. (1993). Testing intervarietal substitution lines in wheat seedlings for tolerance of five to seven days of flooding, Poysa (1984) found that the homologous group five chromosomes were associated with positive effects on seedling survival. Taeb et al. (1993) tested a number of *Triticeae* species for tiller number, shoot dry matter production, and root penetration in waterlogged soil. Using these criteria they found

Thinopyrum elongatum and *Elytrigia repens* to have better tolerance than wheat. The presence of chromosomes 2E and 4E of *Th. elongatum* was associated with a positive effect on root growth in waterlogged conditions.

Boru (1996) studied the segregation ratios of all possible crosses between three waterlogging tolerant spring wheat lines and two sensitive cultivars. He estimated four genes to be responsible for waterlogging tolerance. Alcohol fermentation genes, such as *Adh* found in wheat (Hart, 1980; Waters et al., 1991), barley (Good and Crosby, 1989), and rice (Umeda and Uchimiya, 1994) are frequently associated with waterlogging tolerance.

Although progress has been made in identifying some of the genes responsible for waterlogging tolerance, little is known about the heritability of waterlogging tolerance in general, and in wheat in particular. In the absence of a reliable marker, different morphological and physiological traits have been used in genetic studies for waterlogging tolerance. Most of these traits are quantitative and their expression is usually under strong environmental influences. Therefore, their genetic control is confounded by environmental stress. By studying the heritability of these traits, it is possible to account for genetic and non-genetic factors influencing waterlogging tolerance, and evaluate traits as selection indicators. The objectives of this study were: 1) to estimate heritability of waterlogging tolerance for yield and other traits of wheat under waterlogging stress in early generations, and 2) to provide selection criteria for waterlogging tolerance in wheat breeding programs.

3.2 Materials and Methods

Four segregating soft red winter wheat populations in the F_2 generation were used to estimate heritability of yield and yield components under waterlogging. The initial genetic material was derived from wheat breeding program of Louisiana Agricultural Experiment Station (LAES), Agricultural Center, Louisiana State University.

3.2.1 The Genetic Populations

The initial F_2 segregating population were derived as:

Population 1: TCHERE/SAVANNAH//GA 85240

Population 2: TCHERE/SAVANNAH//PIONEER 2643

Population 3: TCHERE/DS2368//GA 85240

Population 4: TCHERE/DS2368//PIONEER 2691

Tchere is known to be waterlogging tolerant but very susceptible to disease, especially leaf rust (caused by *Puccinia triticina* Eriks.), while DS 2368 was included as a sensitive genotype to waterlogging (S.A. Harrison, personal communication). Genotypes Savannah, GA 85240, Pioneer 2643 and Pioneer 2691 are used as parental components because of their high yield performance in wheat trials (Harrison et al., 1997).

In 1996, seed from all four crosses was planted in Styrofoam nursery trays in the greenhouse, and thinned to one plant per cell. After four weeks from germination, plants were transferred to the field at the Ben Hur Research Farm, LAES Central Station, in Baton Rouge. Plots were 5.0 m x 2.0 m. Plants were widely spaced (40 cm between rows and 20 cm between plants in a row) to produce enough seed for planting the experiment next year. Plants that were late-maturing and those that had disease incidence, were eliminated from the study. About 120 to 150 plants were grown for each population, and 20 were chosen and hand harvested separately, to produce $F_{2,3}$ families.

The genetic structure of families was full-sib within each individual population, and half-sib within population 1 and 2 and within population 3 and 4. Since some cultivars were involved as parental components in several populations, a degree of relationship exists among all the families considered together.

The 80 families in 1997-98 were $F_{2,3}$ i.e., F_2 derived F_3 families, since no selection was applied to the base population of 120-150 F_2 plants per population. In 1998-99 season, the 80 families were $F_{2,4}$, and in 1999-00 season, they were $F_{2,5}$. Therefore, all the results on genetic variance components and heritability estimates will refer to the F_2 base populations. Since, no selection was applied during the four years of study, the variation among F_2 derived lines possesses the same amount of additive variance, regardless of the generations F_3 , F_4 or F_5 of measurement (Cockerham, 1963).

This heritability study was based on the following genetic assumptions:

- 1) Parents involved in crosses are homozygous.
- 2) No relationship exists among the six genotypes involved in crosses.
- 3) Populations from each cross are large enough, so that genetic drift is zero.
- 4) No epistatic interaction of additive x additive, additive x dominance and dominance x dominance exists.

3.2.2 Materials and Designs

The experiment was conducted during 1997-98, 1998-99, and 1999-00, at the Ben Hur Research Farm, LAES Central Station, in Baton Rouge. 80 families from four populations were evaluated in a randomized complete block design with three replications under the effect of five weeks of waterlogging stress. In each replication, each family was

Figure 3.1. Heritability experiment with 80 families derived from four populations under waterlogging conditions, conducted in 1999-2000, at Ben Hur Research Farm, in Baton Rouge.

planted in a three-row plot, with 22 cm row spacing x 1 m length. Soil type was a Commerce silt loam (fine silty, mixed, nonacid, thermic Aeric Fluvaquent). Pre-plant fertilizer at a rate of 240 kg ha⁻¹ of N-P-K and clorsulfuron herbicide (Glean) at 53 g a. i. ha⁻¹ were applied. Waterlogging started at 4-6 leaf stage, and it was realized by pumping water into the plots. Soil was kept wet and muddy by continuous flooding. A top dressing of 90 kg ha⁻¹ N was applied immediately after the waterlogging period ended.

Soil oxygen content was measured using gas samplers buried in the soil at a depth of 10 cm in every replication. Redox potential measurements were taken weekly, during the waterlogging period. Gas samples of 20 ml were drawn, and oxygen concentration was measured using a probe as described by Musgrave (1994).

Data were taken on the mid-row of each plot. Chlorophyll content was the mean of measurements on three random plants per plot, taken immediately after the waterlogging period ended. Height and kernel number were the mean of measurements taken from three random plants. Tiller number was measured by counting the number of heads in a 20 cm length row. Kernel weight was determined from a 100 seed sample for each plot. Yield was measured by hand harvesting and threshing the mid-row.

3.2.3 REML to Estimate Genetic Variance Components

The traditional quantitative genetic methods of estimating additive and dominance variance based on the least square method (ANOVA), require a number of restrictions for the way full and half-sibs are produced. These restrictions make it difficult from the practical point of view to realize all the required crosses, especially in self-pollinated crops, such as wheat. More commonly, the mating designs in plant breeding are complicated and involve more than two parents, and offspring from different populations (crosses), have a degree of relationship. In these cases, the coancestry coefficients differ between any two populations and variance components can not be estimated using ANOVA. Even in the case of pure full and half-sib structure, negative variance components may result in some cases because of the procedure based on the differences among mean squares. When the data are unbalanced, the properties of the variance component estimators are unknown (Searle et al. ,1992).

Mixed model equations (Henderson, 1975; Harville, 1977) provide maximum likelihood estimators of variance components. Such estimators do not place any special demand on the mating design and they can be used for any pedigree.

A mixed model approach was applied to estimate genetic variance components of 80 entries studied in three environments, i.e., years (1998, 1999 and 2000), fitted as:

$$y = X\beta + Z_1\alpha + Z_2\gamma + Z_3\delta + \epsilon \quad [21]$$

where:

y is a vector of $n \times 1$ observations, n is the number of observations for each entry in each year. X and β are the design matrix and the vector of trial effects (including environments and reps within environments). β is a $b \times 1$ vector of fixed effects, where $b = e \times r$, and $1 < e < 3$ is the number of environment, and $1 < r < 3$ is the number of reps within environments. Z_1 and α are the design matrix and vector of populations estimating additive effects, where α is a vector of $a \times 1$, and $1 < a < 4$ is the number of populations. Z_2 and γ are the design matrix and vector of dominance effects, where γ is a $d \times 1$ vector, and $1 < d < 4$ is the number of populations. Z_3 and δ are the design matrix and vector of GE interaction effects, where δ is a $g \times 1$ vector, and $1 < g < 240$ is the cross combination of entries with environments; ϵ is the vector of experimental error effects.

In model [21] environments and reps within environments are considered fixed and are included in the β vector. In this study we are not interested in environments or reps(environments) but we need to separate their effect from the genetic component effects.

The assumptions for random effects are: additive effects are $N(0, \sigma_A^2)$, dominance effects are $N(0, \sigma_D^2)$, GE interaction effects are iid $N(0, \sigma_{GE}^2)$, and errors are iid $N(0, \sigma_\epsilon^2)$.

Random effects have the following variance-covariance matrix:

$$\text{Var} \begin{pmatrix} \alpha \\ \gamma \\ \delta \\ \epsilon \end{pmatrix} = \begin{pmatrix} A\sigma_A^2 & 0 & 0 & 0 \\ 0 & D\sigma_D^2 & 0 & 0 \\ 0 & 0 & I\sigma_{GE}^2 & 0 \\ 0 & 0 & 0 & I\sigma_\epsilon^2 \end{pmatrix} \quad [22]$$

where:

A is a matrix of 80 x 80. The diagonal elements of **A** are equal to 1 and the off-diagonal elements are equal to the two times coancestry coefficient ($2r_{xy}$) between 80 entries in the study. This matrix is obtained by using PROC INBREED of SAS.

D is a matrix of 80 x 80 with diagonal elements equal to double coancestry coefficients within full-sib families and off-diagonal elements the value of double coancestry coefficients among 80 entries.

I is an identity matrix.

The variance-covariance structure in [22] assumes genetic random effects to be related within them (by the coancestry coefficient or double coancestry coefficient) but uncorrelated between them, i.e., additive with dominance effects, while non-genetic random effects are assumed to be independent within the respective source of variation and uncorrelated with other sources of random effects (genetic or non-genetic). If,

$$\hat{\mathbf{u}} = (\hat{\alpha}', \hat{\delta}', \hat{\gamma}') \quad \text{than} \quad \text{var}(\hat{\mathbf{u}}) = \mathbf{G}$$

$$\mathbf{G} = \begin{pmatrix} \mathbf{G}_1 & 0 & 0 & 0 \\ 0 & \mathbf{G}_2 & 0 & 0 \\ 0 & 0 & \mathbf{G}_3 & 0 \\ 0 & 0 & 0 & \mathbf{R} \end{pmatrix}$$

where, $\mathbf{G}_1 = \mathbf{A}\sigma_A^2$ is the covariance matrix of additive effects, $\mathbf{G}_2 = \mathbf{D}\sigma_D^2$ is the covariance matrix of dominance effects, $\mathbf{G}_3 = \mathbf{I}\sigma_{GE}^2$ is the covariance matrix of GE interaction, $\mathbf{R} = \text{Var}(\epsilon) = \mathbf{I}\sigma_\epsilon^2$, is the covariance matrix of errors.

The vector of observations $\mathbf{y}$ is assumed to be multivariate normal (Searle et al., 1992) with mean:

$$E(\mathbf{y}) = \mathbf{X}\boldsymbol{\beta}$$

and variance covariance:

$$\text{Var}(\mathbf{y}) = \mathbf{Z}_1\mathbf{G}_1\mathbf{Z}_1' + \mathbf{Z}_2\mathbf{G}_2\mathbf{Z}_2' + \mathbf{Z}_3\mathbf{G}_3\mathbf{Z}_3' + \mathbf{R} \quad [23]$$

$$\text{or, } \text{Var}(\mathbf{y}) = \mathbf{Z}\mathbf{G}\mathbf{Z}' + \mathbf{R} \quad [24]$$

Mixed model equations (Henderson, 1975; Bernardo, 1994) are used to obtain estimates of α , β , γ , and δ . This approach is important in plant breeding because it provides estimations of fixed effects through best linear unbiased estimators (**BLUE**), predictors for random effects through best linear unbiased predictors (**BLUP**) and variance components. For this study the estimates of α , β , γ , and δ can be obtained by solving the following system of mixed model equations:

$$\begin{pmatrix} \mathbf{X}'\hat{\mathbf{R}}^{-1}\mathbf{X} & \mathbf{X}'\hat{\mathbf{R}}^{-1}\mathbf{Z}_1 & \mathbf{X}'\hat{\mathbf{R}}^{-1}\mathbf{Z}_2 & \mathbf{X}'\hat{\mathbf{R}}^{-1}\mathbf{Z}_3 \\ \mathbf{Z}_1'\hat{\mathbf{R}}^{-1}\mathbf{X} & \mathbf{Z}_1'\hat{\mathbf{R}}^{-1}\mathbf{Z}_1 + \mathbf{G}_1^{-1} & \mathbf{Z}_1'\hat{\mathbf{R}}^{-1}\mathbf{Z}_2 & \mathbf{Z}_1'\hat{\mathbf{R}}^{-1}\mathbf{Z}_3 \\ \mathbf{Z}_2'\hat{\mathbf{R}}^{-1}\mathbf{X} & \mathbf{Z}_2'\hat{\mathbf{R}}^{-1}\mathbf{Z}_1 & \mathbf{Z}_2'\hat{\mathbf{R}}^{-1}\mathbf{Z}_2 + \mathbf{G}_2^{-1} & \mathbf{Z}_2'\hat{\mathbf{R}}^{-1}\mathbf{Z}_3 \\ \mathbf{Z}_3'\hat{\mathbf{R}}^{-1}\mathbf{X} & \mathbf{Z}_3'\hat{\mathbf{R}}^{-1}\mathbf{Z}_1 & \mathbf{Z}_3'\hat{\mathbf{R}}^{-1}\mathbf{Z}_2 & \mathbf{Z}_3'\hat{\mathbf{R}}^{-1}\mathbf{Z}_3 + \mathbf{G}_3^{-1} \end{pmatrix} \begin{pmatrix} \hat{\beta} \\ \hat{\alpha} \\ \hat{\gamma} \\ \hat{\delta} \end{pmatrix} = \begin{pmatrix} \mathbf{X}'\hat{\mathbf{R}}^{-1}\mathbf{y} \\ \mathbf{Z}_1'\hat{\mathbf{R}}^{-1}\mathbf{y} \\ \mathbf{Z}_2'\hat{\mathbf{R}}^{-1}\mathbf{y} \\ \mathbf{Z}_3'\hat{\mathbf{R}}^{-1}\mathbf{y} \end{pmatrix}$$

Substituting in the above mixed model system:

$$\mathbf{G}_1 = \mathbf{A}\hat{\sigma}_A^2, \mathbf{G}_2 = \mathbf{D}\hat{\sigma}_D^2, \mathbf{G}_3 = \mathbf{I}\hat{\sigma}_{GE}^2, \text{ and } \mathbf{R} = \mathbf{I}\hat{\sigma}_\epsilon^2$$

The vector of fixed and random effects will be obtained as:

$$\begin{pmatrix} \hat{\beta} \\ \hat{\alpha} \\ \hat{\gamma} \\ \hat{\delta} \end{pmatrix} = \begin{pmatrix} \mathbf{X}'\mathbf{X} & \mathbf{X}'\mathbf{Z}_1 & \mathbf{X}'\mathbf{Z}_2 & \mathbf{X}'\mathbf{Z}_3 \\ \mathbf{Z}_1'\mathbf{X} & \mathbf{Z}_1'\mathbf{Z}_1 + \mathbf{A}^{-1}\hat{\sigma}_\epsilon^2 / \hat{\sigma}_A^2 & \mathbf{Z}_1'\mathbf{Z}_2 & \mathbf{Z}_1'\mathbf{Z}_3 \\ \mathbf{Z}_2'\mathbf{X} & \mathbf{Z}_2'\mathbf{Z}_1 & \mathbf{Z}_2'\mathbf{Z}_2 + \mathbf{D}^{-1}\hat{\sigma}_\epsilon^2 / \hat{\sigma}_D^2 & \mathbf{Z}_2'\mathbf{Z}_3 \\ \mathbf{Z}_3'\mathbf{X} & \mathbf{Z}_3'\mathbf{Z}_1 & \mathbf{Z}_3'\mathbf{Z}_2 & \mathbf{Z}_3'\mathbf{Z}_3 + \mathbf{I}\hat{\sigma}_\epsilon^2 / \hat{\sigma}_{GE}^2 \end{pmatrix}^{-1} \begin{pmatrix} \mathbf{X}'\mathbf{y} \\ \mathbf{Z}_1'\mathbf{y} \\ \mathbf{Z}_2'\mathbf{y} \\ \mathbf{Z}_3'\mathbf{y} \end{pmatrix}$$

$$= \begin{pmatrix} \mathbf{C}_{00} & \mathbf{C}_{01} & \mathbf{C}_{02} & \mathbf{C}_{03} \\ \mathbf{C}_{10} & \mathbf{C}_{11} & \mathbf{C}_{12} & \mathbf{C}_{13} \\ \mathbf{C}_{20} & \mathbf{C}_{21} & \mathbf{C}_{22} & \mathbf{C}_{23} \\ \mathbf{C}_{30} & \mathbf{C}_{31} & \mathbf{C}_{32} & \mathbf{C}_{33} \end{pmatrix} \begin{pmatrix} \mathbf{X}'\mathbf{y} \\ \mathbf{Z}_1'\mathbf{y} \\ \mathbf{Z}_2'\mathbf{y} \\ \mathbf{Z}_3'\mathbf{y} \end{pmatrix}$$

REML function were used to obtain estimates of β and $\mathbf{G}$. REML estimates for genetic variance components (additive and dominance) and for non-genetic variance components (error and GE interaction) can be obtained by iterating on:

$$\hat{\sigma}_A^2 = (\alpha \mathbf{A}^{-1} \hat{\alpha} + \hat{\sigma}_\varepsilon^2 \text{tr} \mathbf{A}^{-1} \mathbf{C}_{11}) / a \quad [25]$$

$$\hat{\sigma}_D^2 = (\hat{\gamma} \mathbf{D}^{-1} \hat{\gamma} + \hat{\sigma}_\varepsilon^2 \text{tr} \mathbf{D}^{-1} \mathbf{C}_{22}) / d \quad [26]$$

$$\hat{\sigma}_{GE}^2 = (\hat{\delta} \mathbf{I} \hat{\delta} + \hat{\sigma}_\varepsilon^2 \text{tr} \mathbf{C}_{33}) / g \quad [27]$$

$$\hat{\sigma}_\varepsilon^2 = [\mathbf{y}'\mathbf{y} - \hat{\beta}'\mathbf{X}'\mathbf{y} - \hat{\mathbf{u}}'\mathbf{X}'\mathbf{y}] / (n - b) \quad [28]$$

Starting values were given to variance components in order to solve for the vector of effects using mixed model equations, then the estimates of effects were used to calculate the variance components using eq. [25] to [28]. This procedure is iterated many times until convergence is achieved. A program in SAS Proc IML was written for the REML procedure to estimate additive and dominance variance components (Collaku, 2000).

3.2.4 Heritability and Selection Estimates

Narrow sense heritability was estimated on a plot basis. Since phenotypic observations were based on a randomized complete design with $r=3$ replications, and $l=3$ years (environments) heritability estimates were calculated as:

$$h^2 = \hat{\sigma}_A^2 / \hat{\sigma}_P^2 = (\sigma_A^2 + \hat{\sigma}_D^2 + \hat{\sigma}_{GE}^2 / l + \hat{\sigma}^2 / rl)$$

Estimates of additive and dominance variance components and their ratio (heritability) are point estimates. When interpreting heritability estimate values it is important to refer to its precision by giving the standard error and confidence intervals. In this study the standard error of heritability was calculated as:

$$SE(\hat{H}) = SE(\hat{\sigma}_A^2) / \hat{\sigma}_P$$

$$\hat{\sigma}_A^2 \text{ is the additive variance, and } \hat{\sigma}_P = (\hat{\sigma}_P^2)^{1/2} = (\sigma_A^2 + \hat{\sigma}_D^2 + \hat{\sigma}_{GE}^2 / l + \hat{\sigma}^2 / rl)^{1/2} \quad 64$$

$$\hat{\sigma}_A^2 \text{ is the additive variance, and } \hat{\sigma}_P = (\hat{\sigma}_P^2)^{1/2} = (\sigma_A^2 + \hat{\sigma}_D^2 + \hat{\sigma}_{GE}^2 / l + \hat{\sigma}^2 / rl)^{1/2}$$

The distribution of $\hat{\sigma}_P^2$ is known (Bridges et al., 1991), therefore, $\hat{\sigma}_P$ is used in the denominator of standard error of heritability. Standard errors of REML estimates of $\hat{\sigma}_A^2$ are used in the numerator, which are the square root of the diagonal elements of the inverse of Fisher's information matrix (Searle et al., 1992).

Based on heritability estimates and values of phenotypic variances, selection response was calculated as: $R = ih^2 \hat{\sigma}_P^2$, for 5% and 10% selection intensity. Assuming a normal distribution and a truncated selection for the phenotypic values of traits studied, values of selection intensity were $i(5\%) = 2.063$ and $i(10\%) = 1.755$ (Falconer, 1989).

To find traits other than yield as selection criteria for waterlogging tolerance, correlated response to selection was calculated, expressing the expected response in yield if the selection would have been applied for yield components.

Genetic correlation coefficients (Johnston et al., 1955) were calculated as:

$$r = \frac{Cov_{XY}}{\sqrt{\hat{\sigma}_{A(X)}^2 \hat{\sigma}_{A(Y)}^2}}$$

where Cov_{xy} is the additive covariance between two traits X and Y. Correlation coefficients were used to calculate the correlated response as:

$$CR_{Y/X} = ih_x h_y r_{xy} \hat{\sigma}_{XY}$$

where $CR_{Y/X}$ is the expected selection response in yield if the selection was applied for trait X, h_x and h_y are the square root of heritability estimates of yield and trait X.

Values of additive covariances between yield and yield components, as well as values of additive and phenotypic variances, were used to construct selection indices, in order to find the best combination of traits for the maximal yield response under waterlogging tolerance.

3.3 Results and Discussion

The heritability experiment was flooded and maintained under waterlogging stress for 5 weeks, starting at the 4-6 leaf stage. Redox potential data range from 297 to 326 mV (Table 3.1). They are similar to redox potential data taken in flooded plots for the yield loss study experiment, where yield mean losses from waterlogging averaged 44%. Heritabilities were estimated under waterlogging stress, evaluating the degree to which the hereditary factors determine waterlogging tolerance for yield and yield components.

Table 3.1. Redox potential data from five weeks of waterlogging of 80 families from four wheat populations in the heritability experiment.

Period	Redox potential (mV)								
	1997-98			1998-99			1999-00		
	Rep 1	Rep 2	Rep 3	Rep 1	Rep 2	Rep 3	Rep 1	Rep 2	Rep 3
Week 1	307	315	326	304	308	298	315	309	304
Week 2	302	303	300	315	321	309	303	317	312
Week 3	315	324	325	313	302	324	318	313	317
Week 4	317	306	319	304	297	317	322	304	311
Week 5	303	332	305	312	311	322	316	309	306

3.3.1 Estimation of Additive and Dominance Variance

Traditional mating designs for estimating genetic variance components are applicable if the parental components of populations are unrelated. In this study, which is common in breeding programs, some of the parents were involved in several population, and the families derived from these populations had a degree of relationship. By using REML procedure (Henderson, 1975; Harville 1977) for estimating genetic variance components, it is possible to account for the relationship among derived families. A covariance matrix **A** of additive effects $\hat{\alpha}$ and a covariance matrix **D** of dominance effects $\hat{\delta}$ were calculated. The diagonal elements of **A** are 1, and the off-diagonal elements are equal to $r=2f_{XY}$, where f_{XY} is the coancestry coefficient between two families.

Table 3.2. Covariance matrix **A** of additive effects.

	1	...	20	21	...	40	41	...	60	61	...	80
1	1											
20	.5	1										
21			1									
40			.5	1								
41					1							
60					.5	1						
61							1					
80							.5	1				

Off-diagonal elements of **A** matrix are 0.5 between full-sib families, i.e., between families 1 to 20, 21 to 40, 41 to 60, and 61 to 80. These values become smaller as the relationship between entries becomes weaker.

Covariance matrix **D** for dominance effects is given in Table 3.3. Elements of this matrix are double coancestry coefficients (u). Diagonal elements are 0.25 as double coancestry coefficients among full-sib families. Some off-diagonal elements are greater than 0 depending on the relationship among different groups of full-sib families.

Table 3.3. Covariance matrix **D** of dominance effects.

1 ... 20	21 ... 40	41 ... 60	61 ... 80
.25	0	0	0
20			
21	.25	.0625	0
40			
41	.625	.25	0
60			
61	0	0	.25
80			

The above two matrices show different relationships among 80 families. Such relationships should be taken into account when estimating genetic variance components. Bromley et al. (2000) noted that ignoring these relationships has usually resulted in a reduction of estimated values of genetic variances. Data of these two matrixes were

appended in the proc mixed program, to estimate additive and dominance variance based on mixed model approach [22].

Table 3.4. REML estimates of additive and dominance variance from 80 families derived without selection from four soft winter wheat population.

Trait	$\hat{\sigma}_A^2$	std.err. of $\hat{\sigma}_A^2$	$\hat{\sigma}_D^2$	$\hat{\sigma}_{FY}^2$	$\hat{\sigma}_\epsilon^2$
Yield	140.21	9.71	214.51	551.81	136.22
Chlorophyl	3.98	0.36	1.32	9.82	3.91
Height	36.90	10.10	32.20	48.73	10.93
Kernel weight	0.15	0.01	0.11	0.09	0.03
Kernel number	9.89	0.80	25.12	17.62	6.91
Tiller number	10.23	1.19	13.63		25.54

The presence of both additive and dominance variance for all the traits studied was anticipated, since populations were in F_2 . The absolute value of the additive variance component was greater than the dominance variance component for kernel weight, chlorophyl content, and height. For yield, kernel and tiller number, the additive variance component was smaller than the dominance component, showing that these three last traits are under a stronger control by dominance effects. Selecting for yield, or kernel number in early generations under waterlogging stress, would not be as effective as selecting for traits such as kernel weight or chlorophyl content. GE interaction, i.e., interaction of families with environments is an important component of variance for all traits studied. Relative importance of this variance component for yield was greater than for other traits, accounting for 53% of the total variability. As shown in earlier studies for wheat under

stress conditions (Tillman and Harrison, 1996), the magnitude of genotype by environment interaction is important in the case of severe conditions, and it can be a source of bias in heritability estimates, especially for yield.

3.3.2 Heritability of Yield and Yield Components Under Waterlogging Stress

In the presence of additive and dominance variance, narrow sense heritability estimates are required to make predictions about the selection response. From the traits studied, the highest heritability estimate of 0.54 was found for height (Table 3.5). Another important property required for heritability estimates is precision, estimated by the standard error. High values of standard error for heritability estimates of height and yield are an indicator of poor precision of heritability. In this context heritability estimates for yield and height are suspicious, since the parametric value may range in a wide confidence interval due to very large values of standard error.

Table 3.5. Heritability estimates and expected selection response for yield, chlorophyll content, height, tiller number, kernels/head and kernel weight under waterlogging stress.

Traits	h^2	std.err. of h^2	$R_{(5\%)} / \bar{X}$ (%)†	$R_{(10\%)} / \bar{X}$ (%)‡
Yield	0.25	0.41	11	10
Chlorophyll	0.37	0.11	20	17
Height	0.54	1.22	12	10
Kernel weight	0.47	0.02	17	14
Kernel number	0.22	0.12	10	9
Tiller number	0.31	0.34	18	15

† Expected response from 5% selection [$R_{(5\%)}$] expressed in percent of the mean value ($\bar{X}$).

‡ Expected response from 10% selection [$R_{(10\%)}$] expressed in percent of the mean value ($\bar{X}$).

Considering the low value of heritability estimate for yield (0.25), and its high values of standard error, it is obvious that selecting for yield in early generation is not a good breeding strategy.

Heritability of number of kernels per head was the lowest of all the traits (0.22). In previous studies (Knot and Talukdar, 1971; Cantrell and Haro-Arias, 1986), kernel number was found to be highly heritable. Moreover, it has been suggested that this trait is controlled by a relatively small number of genes (Islam et al., 1985). Low values of heritability estimate found in this study are probably due to waterlogging stress. In previous studies in wheat (Collaku, 1994), and in soybean (Kristin et al., 1997) it has been found that traits depressed the most by environmental stress had the lowest value of heritability. As found in the first part of this study (losses from waterlogging), yield and kernel number were the most sensitive traits to waterlogging. Under environmental stress the phenotypic variance of these traits generally increases more rapidly than the genotypic variance (Johnston and Frey, 1967), resulting in a reduced heritability.

Heritability of tiller number was greater than heritability of yield, but lower than the heritability values of height, kernel weight, and chlorophyll content. Hucl and Baker (1991) have found a polygenic inheritance for tiller number. They found that heritability of this trait was greatly reduced under drought conditions. Under waterlogging effects, the response of genotypes for tiller number resulted among the most sensitive ones, with a 44% reduction.

Expected selection response is another useful estimate when comparing traits as selection criteria. To obtain comparable estimator for traits measured in different units, values of expected selection response were expressed in percentage of the respective

mean. A response 20% higher than the mean is expected from direct selection of 5% intensity on chlorophyll (Table 12). High values of selection response were observed for kernel number (17%) and tiller number (18%). Values of expected selection response are valid for selection for traits per se, but considered simultaneously with heritability estimates they constitute valid indicators for traits to be used in early generation selection. A highly heritable, easily measured trait can be used for a rapid screening of a large number of families in early generations. Nass (1987) found early selection for large seed size to be more effective than three other selection methods. Based on the results of this study it seems that selecting for kernel weight, chlorophyll content, or tiller number could be used to screen families for waterlogging tolerance. In some cases direct selection for yield components, such as kernels/head and kernel weight was more effective than selection for yield per se (Islam et al., 1985; Gebre-Mariam et al., 1988).

3.3.3 Genetic Correlations

The ability to identify other traits that can effectively be used as selection criteria in early generation requires comparison of their correlated response, which depend largely on the heritability of the traits and their genetic correlation with yield. From Table 3.6, strong genetic correlations were observed between yield and tiller number ($r=1.00$), yield and seed weight ($r=0.56$), and yield and chlorophyll ($r=0.40$). These relationships and high values of heritability, make these traits important criteria for indirect selection in early generation. Kernel number per head showed a relatively high correlation with yield ($r=0.38$), but its importance as a selection criteria is reduced because of a low heritability estimate. This result has been confirmed earlier (Collaku, 1994), where under stress conditions, a weak genetic association of kernel number with yield was found.

Table 3.6. Genetic correlations among yield and five other traits in wheat from a heritability study of 80 families under waterlogging stress.

Trait	Height	Tiller number	Kernel/head	Kernel weight	Yield
Chlorophyll	- 0.06	1	0.04	0.31*	0.40**
Height		0.35**	0.33*	0.18	0.02
Tiller number			0.34**	0.44**	1
Kernel number				0.08	0.38**
Kernel weight					0.56**

Kernel weight had a significant genetic correlation with tiller number ($r=0.44$) and chlorophyll ($r=0.31$), as well as yield, showing that selecting for this trait would notably improve other important traits for yield. Correlations among height and other traits were generally low (Table 3.6). Although it has a high value of heritability, this trait seems to have little effect on yield or other important yield components. In two cases (yield-tiller number and chlorophyll-tiller number), correlation coefficients were 1. These high values of genetic correlation coefficients are probably due to the two different methodologies used for evaluating additive variance components and genetic covariances.

3.3.4 Selection for Waterlogging Tolerance in Wheat

In order to combine information from heritability and genetic correlations in determining the best traits to be used in early generation selection, correlated response (CR) for yield were calculated (Table 3.7).

Table 3.7. Efficiency of correlated selection response for yield estimated from 80 wheat families grown under waterlogging conditions.

Trait to be selected	$CR (i = 10\%)$	$CR (i = 5\%)$	$CR/R (\%)$
Yield - Direct response (R)	10.3	12.1	100
Chlorophyll (CHL)	5.1	6.2	49
Height (H)	0.3	0.4	3
Tiller number (T)	11.5	13.5	111
Kernel number (KN)	3.5	4.2	34
Kernel weight (KWT)	7.9	12.1	77

An 11% increase in yield response is expected if we select for tiller number compared to the direct selection for yield. A high correlated response is also expected for kernel weight. The high values of correlated response for these two traits are due to their high heritabilities and strong genetic correlation with yield under waterlogging. Selecting individually for these traits would improve yield. This is important for early generation selection when the genetic material is large. Indirect selection can be advantageous, if the indirect trait can be measured with more accuracy than the primary trait. Often, measurements of the indirect trait are easier than the direct trait, which makes indirect selection a convenient alternative. Therefore selecting for tiller number or kernel weight would be an efficient and practical way of selection for waterlogging tolerant genotypes in wheat.

Genetic information about yield and yield components can be combined together in a selection index, to maximize selection response for yield (Henderson, 1963; Wricke and Weber, 1986; Falconer, 1989). The first report of the use of a selection index in plant

breeding was by Smith (1936). A classic example of index use is given by Brim et al. (1959). Wells and Kofoid (1986) estimated efficiency of selection indices for improving yield, plant height, and protein content of an intermating population of spring wheat. In this method, selection is done simultaneously for multiple traits, based on the values of index weights.

An index is a linear combination of the form:

$$I = \sum b_i X_i \quad [29]$$

where X_i is the observed value of trait i and b_i is the weight assigned to the trait in the selection index. Economic value of the trait is included in the index to better estimate the selection response.

Expressed in matrix notation, index is calculated as:

$$I = \mathbf{p}'\mathbf{b}$$

where $\mathbf{p}$ is a column vector of phenotypic values X , and $\mathbf{b}$ is a column vector of index weights.

The objective of the index is to optimize the correlation between the predicted value of the phenotypic index, I , and the genotypic or true value, H , where:

$$I = \sum b_i x_i \quad \text{and} \quad H = \sum e_i y_i$$

In the above equations, e_i are the economic weights, and y_i are the genotypic values. Solving the simultaneous equations, gives b_i , such that maximize the correlation between $\mathbf{I}$ and $\mathbf{H}$ (Henderson, 1963; Wricke and Weber, 1986).

In matrix notation, the above relationship would be:

$$\mathbf{PB} = \mathbf{Ge}$$

where $\mathbf{G}$ is the genetic variance-covariance matrix, $\mathbf{e}$ is the vector of economic weights, $\mathbf{P}$ is the phenotypic variance-covariance matrix, and $\mathbf{B}$ is the unknown vector of phenotypic trait weights, or selection indices, b_i . Solving for $\mathbf{B}$ leads to:

$$\mathbf{B} = \mathbf{P}^{-1}\mathbf{Ge} \quad [30]$$

The total response to selection by using the optimum index is:

$$R_I = i(\sum b_i \mathbf{G})^{1/2} \quad [31]$$

The vector of expected selection response from index selection is calculated as:

$R_i = i\mathbf{Gb}/(\mathbf{b}'\mathbf{Pb})^{1/2}$, where i is the selection intensity. Matrixes $\mathbf{P}$ and $\mathbf{G}$ were constructed based on the additive variance estimates, genetic covariances, and phenotypic variance-covariances, to solve for values of selection index in eq.[30]:

$$\mathbf{B} = \begin{pmatrix} 533.7 & 14.8 & 2.97 & 33.2 & 56.0 \\ 14.8 & 10.9 & 0.31 & 3.3 & 7.6 \\ 2.97 & 0.31 & 0.31 & 0.11 & 0.56 \\ 33.2 & 3.3 & 0.11 & 44.9 & 3.84 \\ 56.0 & 7.6 & 0.56 & 3.84 & 33.3 \end{pmatrix}^{-1} \begin{pmatrix} 140.2 & 9.4 & 2.5 & 13.8 & 54.1 \\ 9.4 & 3.98 & 0.24 & 0.28 & 7.3 \\ 2.5 & 0.24 & 0.15 & 0.098 & 0.36 \\ 13.8 & 0.28 & 0.098 & 9.89 & 3.53 \\ 54.1 & 7.33 & 0.36 & 3.53 & 10.2 \end{pmatrix} \begin{pmatrix} 1 \\ 0 \\ 0 \\ 0 \\ 0 \end{pmatrix}$$

The vector of the weights, $\mathbf{b}$, for the above index: Y-CHL-KWT-KN-T resulted:

$\mathbf{B} = (0.082 \quad -0.482 \quad 5.141 \quad 0.142 \quad 1.494)$, with an index response $R_i = 17.85$, for selection intensity of 10% ($i = 1.755$).

Selection indices and their respective index response for all the possible combinations of yield with other traits were calculated, starting with two traits and ending with four traits.

Table 3.8. Predicted response in yield from selection among 80 wheat families grown under waterlogging conditions based upon different selection indices.

Index	$R_I/\bar{X}_Y \dagger$	$R_I/R_Y \ddagger$
	----- % -----	-----
Y	10.0	100
Y-CHL	10.5	107
Y-KWT	11.5	117
Y-KN	10.1	104
Y-T	12.2	125
Y-CHL-KWT	11.7	120
Y-CHL-KN	10.5	107
Y-CHL-T	16.2	165
Y-KWT-T	16.8	172
Y-KN-T	15.1	146
Y-KWT-KN	11.6	118
Y-CHL-KWT-KN	11.7	120
Y-CHL-KWT-T	16.9	173
Y-CHL-KN-T	16.0	164
Y-KWT-KN-T	16.4	170
Y-CHL-KWT-KN-T	16.9	173

† Expected response from selection index, R_I , as a percentage of the yield mean, $\bar{X}_Y$.

‡ Expected response from selection index, R_I , as a percentage of selection response for yield, R_Y .

Selection indices were based on an economic value of 1 for yield and 0 for all yield components. Height was not included in the construction of selection index, since it did not show any important effect on yield or other yield components.

Maximal improvement in yield of about 17% is expected for selection based on Y-CHL-KWT-KN-T, Y-CHL-KWT-T, and Y-KWT-T indices (Table 3.8). Considering yield losses from waterlogging at 44% and assuming that the predicted gains will remain fairly constant for several cycles of selection, then at least three cycles of selection should produce a promising source population for waterlogging tolerance. Use of recurrent selection with the base population of 80 families, would accelerate the selection process maintaining a better balance of genetic variation for yield. Since this process in wheat requires a lot of manual work, it would be more convenient to use Y-KWT-T index, considering yield, kernel weight and tiller number. Kernel weight and tiller number have significant genetic correlation with chlorophyll content, therefore, use of this selection index should contribute to a better yield improvement than direct selection for yield per se, while improving other important characteristics of the plant.

Expected response from selection index based on yield and another trait were not very promising, except for Y-T index (12.2%). The predicted superiority of selection indices based on four or five traits compared to selection index Y-KWT-T was very modest (Table 3.8). In plant breeding practice, it is preferable to use those selection indices that provide maximum improvement with minimum number of traits. Results of this study confirm that the best selection methodology to follow for maximal improvement of waterlogging tolerance, should be that based on Y-KWT-T index.

The claimed gain of selection indices needs to be confirmed in selection practice. Moreover, the relative efficiency of various traits associated with yield depends on environmental conditions of specific breeding programs and on the genotypic variation. The estimated values of genetic variances obtained from 80 families represent a reliable base to start selection for waterlogging tolerance in wheat.

SUMMARY AND CONCLUSIONS

Waterlogging is one of the factors depressing wheat yield. Losses caused by waterlogging in yield and other quantitative traits were measured, in order to determine their relative importance as indicators of waterlogging tolerance. Yield and yield component response had a linear reduction to different duration of waterlogging. Yield losses from waterlogging evaluated in field conditions averaged 44%, due mainly to a combined effect of reduced tiller and kernel number. Screening of wheat genotypes for waterlogging tolerance identified the potential for waterlogging tolerance in breeding material. Genotypes Terral LA 422, Shelby, and Pioneer 26R61 were the most waterlogging tolerant. When screening for waterlogging tolerance, it is important to study the direction and magnitude of genotype by waterlogging stress interaction. Some of the high yielding genotypes in normal conditions, such as Coker 9663, FFR 502W, had a large yield reduction from waterlogging, as a result of a large genotype by waterlogging interaction.

Since the quantitative traits used as indicators of waterlogging tolerance are under a strong environmental influence, heritability estimates were obtained to separate heritable from non-heritable factors related to waterlogging tolerance. Restricted Maximum Likelihood (REML) procedure was used to estimate genetic variance components of additive and dominance effects. REML method is advantageous over traditional quantitative genetic methods because it provides an estimation of additive and dominance variance components without any restriction in mating design. The 80 families used in this study had a degree of relationship among them. For this case, that is

common in plant breeding, the traditional designs would have failed to accurately estimate genetic variance components.

High values of heritability were observed for some yield components, such as kernel weight, and chlorophyll. Low values of heritability for yield were associated with high values of standard error, indicating a wide confidence interval and low precision, therefore, yield selection in early generation would not be an effective and safe breeding alternative. Some of the yield components such as kernels per head, had low value of heritability due to a higher sensitivity to waterlogging stress.

The success in yield response when selecting for yield components, depends largely on heritability of yield components and their genetic correlation with yield. Strong genetic correlations were observed between yield and kernel weight and yield with tiller number. Under waterlogging conditions, these traits are important selection indicators for yield because they have the highest correlated response among yield components. Selecting for tiller number or kernel weight would be an effective way to improve yield, especially in early generation when a large genetic material exists.

Selection indices were constructed in order to make use of a strong genetic correlation between yield and some yield components, such as tiller number and kernel weight, that had high heritability values. A maximal improvement of 17% in yield is expected from selection based on yield-kernel weight-tiller number index. At least three cycles of selection would be needed to produce promising source populations for waterlogging tolerance by using this index. Selection based on yield-kernel weight-tiller number index would be preferable over selection based on yield-chlorophyll-kernel

weight-tiller number index or yield-chlorophyll-kernel weight-kernel number-tiller number index, since maximal improvement could be achieved with a minimum number of traits to be selected. This selection strategy would contribute to a better yield improvement than direct selection for yield per se, while improving at the same time other important plant characteristics, due to strong correlation of tiller number and kernel weight with other yield components.

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APPENDIX 1

DATA OF SHELTER EXPERIMENT

ENT	YR	REP	TRT	CHL.1	CHL.2	CHL.3	CHL.4
1	1	1	1	30.5	42.5	34.8	32.1
2	1	1	1	31.8	35.4	39.8	41.0
3	1	1	1	39.7	38.4	48.5	43.2
4	1	1	1	28.6	35.0	28.9	31.7
5	1	1	1	36.5	40.0	39.5	49.3
6	1	1	1	35.2	33.0	29.4	37.1
7	1	1	1	26.3	35.4	30.8	40.7
8	1	1	1	33.8	31.4	26.4	32.8
9	1	1	1	38.5	38.4	41.1	38.6
10	1	1	1	34.0	40.0	32.7	47.2
1	1	1	2	34.8	31.3	21.9	27.1
2	1	1	2	35.7	33.3	30.9	30.0
3	1	1	2	41.8	30.6	29.0	37.5
4	1	1	2	31.6	28.1	26.7	28.4
5	1	1	2	37.4	33.3	29.0	24.5
6	1	1	2	32.8	28.5	19.1	35.3
7	1	1	2	24.5	27.2	25.0	36.9
8	1	1	2	26.5	30.4	22.0	27.1
9	1	1	2	33.3	36.0	27.8	29.2
10	1	1	2	35.6	28.1	30.6	34.3
1	1	1	3	26.6	30.1	20.9	20.0
2	1	1	3	31.0	32.5	20.1	24.0
3	1	1	3	38.5	35.3	22.9	37.2
4	1	1	3	31.3	29.2	20.0	14.1
5	1	1	3	34.5	31.9	22.2	32.6
6	1	1	3	28.6	28.7	17.1	26.1
7	1	1	3	22.0	26.3	18.5	24.3
8	1	1	3	32.2	31.0	18.4	23.3
9	1	1	3	35.4	36.0	15.1	21.0
10	1	1	3	34.5	32.9	18.8	18.1
1	1	1	4	32.9	29.7	23.0	5.3
2	1	1	4	41.0	30.4	24.2	4.3
3	1	1	4	40.0	30.1	28.2	16.3
4	1	1	4	33.5	28.8	23.7	9.6
5	1	1	4	36.9	30.1	16.7	4.3
6	1	1	4	29.5	31.4	16.0	9.1
7	1	1	4	36.1	32.3	20.4	16.5
8	1	1	4	38.9	27.6	21.7	12.5
9	1	1	4	37.5	33.5	24.9	12.0
10	1	1	4	35.9	31.5	24.5	8.1

ENT	YR	REP	TRT	CHL.1	CHL.2	CHL.3	CHL.4
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1	1	2	1	31.3	36.4	34.8	32.1
2	1	2	1	35.3	44.7	40.8	42.0
3	1	2	1	39.7	47.9	41.0	50.4
4	1	2	1	29.8	37.4	40.0	38.2
5	1	2	1	42.0	40.1	37.1	35.3
6	1	2	1	30.7	33.2	37.1	39.0
7	1	2	1	26.2	34.9	31.3	39.8
8	1	2	1	30.8	36.7	33.7	33.2
9	1	2	1	37.5	44.1	40.8	39.8
10	1	2	1	29.9	39.1	31.9	46.6
1	1	2	2	35.3	30.5	22.7	23.2
2	1	2	2	38.3	34.9	32.5	38.5
3	1	2	2	33.5	35.6	38.0	35.6
4	1	2	2	33.8	31.7	25.8	34.5
5	1	2	2	36.3	34.3	27.8	35.3
6	1	2	2	33.7	29.4	22.2	27.9
7	1	2	2	25.6	28.5	24.6	37.8
8	1	2	2	35.9	29.5	27.4	40.0
9	1	2	2	38.7	38.6	30.7	39.9
10	1	2	2	32.1	36.7	34.8	45.4
1	1	2	3	31.5	32.6	19.6	20.0
2	1	2	3	38.9	29.6	25.4	23.7
3	1	2	3	38.9	32.5	25.2	26.5
4	1	2	3	31.5	30.0	19.9	17.0
5	1	2	3	31.5	27.2	15.5	29.8
6	1	2	3	32.5	29.0	18.2	20.6
7	1	2	3	30.0	24.5	21.0	30.6
8	1	2	3	32.1	28.4	25.3	20.2
9	1	2	3	37.3	31.3	22.4	22.8
10	1	2	3	31.1	34.7	30.0	25.5
1	1	2	4	35.8	27.9	20.2	7.4
2	1	2	4	36.7	34.6	25.0	12.1
3	1	2	4	38.3	36.0	21.0	12.4
4	1	2	4	30.4	31.6	22.5	14.0
5	1	2	4	30.3	32.4	17.6	11.6
6	1	2	4	32.6	28.7	19.6	8.3
7	1	2	4	29.3	28.3	22.1	16.2
8	1	2	4	31.8	32.6	16.7	11.8
9	1	2	4	37.5	30.5	25.9	13.2
10	1	2	4	32.4	31.9	24.2	7.8

ENT	YR	REP	TRT	CHL.1	CHL.2	CHL.3	CHL.4
1	1	3	1	31.4	38.8	38.5	45.4
2	1	3	1	33.2	35.1	34.2	48.1
3	1	3	1	39.3	42.7	40.4	56.7
4	1	3	1	28.8	37.4	38.8	38.2
5	1	3	1	34.4	34.0	31.3	30.8
6	1	3	1	34.2	32.1	35.5	37.9
7	1	3	1	26.2	32.3	35.3	38.2
8	1	3	1	35.2	38.4	33.3	49.4
9	1	3	1	35.9	43.3	28.0	29.7
10	1	3	1	36.2	33.0	35.0	30.0
1	1	3	2	34.9	31.9	22.3	33.0
2	1	3	2	34.1	34.5	27.1	42.5
3	1	3	2	40.0	35.4	35.8	58.8
4	1	3	2	29.4	32.7	22.0	20.0
5	1	3	2	36.1	36.0	21.7	22.6
6	1	3	2	33.3	29.3	27.1	28.0
7	1	3	2	24.0	29.5	27.6	28.1
8	1	3	2	32.2	30.3	33.4	43.8
9	1	3	2	38.0	35.0	26.5	36.3
10	1	3	2	33.9	33.0	28.8	44.0
1	1	3	3	31.5	31.5	22.2	21.3
2	1	3	3	32.3	33.6	23.2	19.7
3	1	3	3	36.2	30.6	19.5	28.3
4	1	3	3	31.5	32.7	22.1	31.9
5	1	3	3	39.2	32.2	21.2	21.8
6	1	3	3	33.5	26.2	18.9	22.4
7	1	3	3	22.0	24.3	19.2	23.9
8	1	3	3	34.0	31.4	24.8	26.2
9	1	3	3	32.6	35.3	24.5	18.2
10	1	3	3	33.8	28.8	23.1	23.3
1	1	3	4	34.5	30.8	24.1	13.0
2	1	3	4	35.1	32.3	25.9	19.6
3	1	3	4	36.6	34.3	26.4	11.2
4	1	3	4	32.0	27.5	24.3	13.9
5	1	3	4	34.1	33.3	21.6	16.7
6	1	3	4	34.5	29.9	22.0	9.1
7	1	3	4	27.7	29.6	20.6	18.0
8	1	3	4	34.0	26.0	21.9	18.0
9	1	3	4	37.9	35.4	22.2	11.0
10	1	3	4	35.7	29.3	21.7	15.0

ENT	YR	REP	TRT	CHL.1	CHL.2	CHL.3	CHL.4	TILLER/P.	HGT	KERNEL/P.	YLD
1	2	1	1	40.8	38.8	39.2	43.2	3	15.0	36	2.75
2	2	1	1	47.1	51.9	46.8	54.0	3	20.0	32	2.73
3	2	1	1	47.3	40.2	38.1	48.8	4	20.0	32	3.40
4	2	1	1	38.5	35.0	35.3	37.1	4	23.0	27	3.04
5	2	1	1	40.6	37.0	37.5	37.9	3	21.0	37	3.38
6	2	1	1	43.0	32.5	36.0	37.2	4	17.5	34	4.11
7	2	1	1	.	.	.	.	.	.	.	.
8	2	1	1	30.7	32.0	36.0	40.5	3	18.0	22	1.74
9	2	1	1	45.7	32.0	38.6	42.6	4	18.0	30	2.44
10	2	1	1	39.6	46.0	43.0	45.4	4	18.0	30	3.82
1	2	1	2	40.2	35.5	38.2	41.6	2	16.0	29	1.91
2	2	1	2	40.2	42.6	42.7	45.9	3	20.0	34	3.38
3	2	1	2	39.0	32.0	38.0	46.2	3	18.5	24	1.73
4	2	1	2	32.7	30.0	36.1	40.8	4	21.0	22	2.67
5	2	1	2	42.9	32.1	32.5	37.7	3	19.5	28	2.39
6	2	1	2	40.4	36.1	35.0	39.8	4	18.0	33	3.56
7	2	1	2	.	.	.	.	.	.	.	.
8	2	1	2	30.0	25.5	32.0	36.5	4	16.0	24	1.90
9	2	1	2	33.9	30.9	39.1	39.9	4	17.5	26	2.71
10	2	1	2	43.7	40.4	39.0	41.9	4	16.5	27	3.33
1	2	1	3	46.3	37.0	29.6	37.8	2	14.0	27	1.71
2	2	1	3	49.9	36.0	28.5	40.1	2	17.0	32	1.63
3	2	1	3	48.6	38.9	33.0	43.6	3	18.0	25	2.46
4	2	1	3	31.9	30.9	29.4	38.0	3	15.0	23	2.38
5	2	1	3	45.0	30.1	29.0	33.2	3	17.0	23	2.35
6	2	1	3	46.3	26.8	25.0	34.7	4	15.0	24	2.82
7	2	1	3	.	.	.	.	.	.	.	.
8	2	1	3	40.0	30.7	26.5	32.3	2	19.0	26	1.71
9	2	1	3	45.8	36.0	28.3	40.5	3	15.0	29	2.74
10	2	1	3	33.8	30.0	28.0	35.0	3	14.0	24	2.30
1	2	1	4	35.9	29.0	28.5	30.0	1	13.5	20	0.60
2	2	1	4	41.1	27.9	28.0	29.5	1	16.5	25	0.74
3	2	1	4	42.9	35.0	33.5	21.5	2	18.0	28	1.78
4	2	1	4	35.3	28.5	26.4	28.2	2	16.0	18	1.01
5	2	1	4	41.5	28.0	24.2	28.3	2	15.5	21	1.23
6	2	1	4	39.8	28.0	26.0	24.5	3	15.0	23	2.09
7	2	1	4	.	.	.	.	.	.	.	.
8	2	1	4	34.6	25.0	24.9	23.0	1	17.5	23	0.83
9	2	1	4	49.2	21.3	20.4	20.8	3	15.0	22	0.71
10	2	1	4	37.4	25.3	23.0	20.3	1	14.0	18	0.90

ENT	YR	REP	TRT	CHL.1	CHL.2	CHL.3	CHL.4	TILLER/P.	HGT	KERNEL/P.	YLD
1	2	2	1	45.0	42.8	41.0	44.3	3	15.5	35	2.80
2	2	2	1	43.3	39.6	40.2	46.1	3	19.0	30	2.71
3	2	2	1	49.4	43.0	38.8	44.1	4	20.0	31	3.30
4	2	2	1	42.5	37.0	37.2	40.0	4	22.0	25	2.97
5	2	2	1	39.0	39.2	39.6	40.0	4	20.0	39	3.17
6	2	2	1	44.4	38.4	38.0	41.4	4	18.0	33	3.94
7	2	2	1	.	.	.	.	.	.	.	.
8	2	2	1	27.0	28.0	32.0	40.4	4	18.0	21	1.89
9	2	2	1	37.6	34.0	35.2	46.5	4	17.5	27	2.68
10	2	2	1	42.6	39.2	39.5	45.3	4	18.0	33	3.51
1	2	2	2	49.2	39.7	39.6	39.0	3	17.0	29	1.88
2	2	2	2	38.5	37.8	41.9	42.2	3	20.0	31	3.65
3	2	2	2	39.3	32.4	36.5	37.5	3	19.0	26	1.64
4	2	2	2	40.6	33.0	33.2	34.9	3	21.0	21	2.57
5	2	2	2	40.3	35.2	32.0	31.0	3	20.0	28	2.44
6	2	2	2	42.2	30.3	34.0	35.1	4	18.0	30	3.36
7	2	2	2	.	.	.	.	.	.	.	.
8	2	2	2	32.1	30.0	30.6	34.1	2	16.0	21	1.66
9	2	2	2	46.8	41.5	40.4	40.1	3	17.0	25	2.39
10	2	2	2	38.3	33.5	34.0	42.0	3	16.0	26	3.12
1	2	2	3	40.9	35.5	33.5	34.8	2	14.0	26	1.84
2	2	2	3	49.9	38.0	33.9	34.5	2	16.0	33	1.74
3	2	2	3	45.0	39.7	29.3	35.5	3	18.0	25	2.35
4	2	2	3	45.1	37.2	31.5	32.5	3	16.0	23	2.40
5	2	2	3	43.6	41.9	31.3	38.2	2	16.5	24	2.11
6	2	2	3	39.6	37.1	33.2	36.2	3	15.5	24	2.57
7	2	2	3	.	.	.	.	.	.	.	.
8	2	2	3	31.3	34.7	25.7	30.8	3	18.0	25	1.84
9	2	2	3	51.5	36.0	31.9	35.3	3	18.0	28	2.55
10	2	2	3	49.4	45.0	32.0	36.3	2	15.0	23	2.11
1	2	2	4	46.9	38.5	33.0	30.0	1	13.0	19	0.75
2	2	2	4	50.6	34.1	34.0	33.8	1	16.0	25	0.78
3	2	2	4	39.5	34.0	27.8	19.9	2	17.0	28	1.94
4	2	2	4	42.0	30.4	28.0	27.7	2	15.5	19	1.15
5	2	2	4	45.2	34.6	24.3	20.7	3	15.5	23	1.14
6	2	2	4	37.8	27.6	26.0	20.3	3	15.0	23	1.89
7	2	2	4	.	.	.	.	.	.	.	.
8	2	2	4	36.0	30.2	30.0	27.8	2	18.0	24	0.97
9	2	2	4	43.6	37.2	29.4	22.0	1	16.0	21	0.54
10	2	2	4	45.0	38.0	27.5	26.9	1	13.0	19	0.86

ENT	YR	REP	TRT	CHL.1	CHL.2	CHL.3	CHL.4	TILLER/P.	HGT	KERNEL/P.	YLD
1	2	3	1	43.4	40.4	41.5	46.5	3	16.0	35	2.39
2	2	3	1	42.0	46.9	45.5	48.0	3	20.0	31	2.37
3	2	3	1	39.0	41.0	40.5	40.4	4	19.0	30	3.31
4	2	3	1	33.4	38.3	40.7	42.0	3	22.0	26	3.16
5	2	3	1	38.4	35.0	34.5	40.2	4	21.0	34	3.11
6	2	3	1	36.2	37.5	38.3	41.5	5	18.0	33	3.94
7	2	3	1	.	.	.	.	.	.	.	.
8	2	3	1	35.7	31.4	33.4	43.8	3	18.0	22	1.89
9	2	3	1	37.6	37.7	39.5	42.0	4	18.0	30	2.35
10	2	3	1	44.7	39.7	38.5	44.8	4	17.5	30	3.96
1	2	3	2	45.7	37.0	30.0	32.0	2	16.5	29	1.74
2	2	3	2	49.0	29.5	33.6	34.1	3	20.0	33	3.21
3	2	3	2	48.9	32.4	34.5	35.6	2	19.0	25	1.54
4	2	3	2	36.0	28.4	28.0	30.4	3	20.5	24	2.38
5	2	3	2	44.4	24.0	27.2	29.3	3	20.0	29	2.51
6	2	3	2	38.0	25.5	25.0	24.0	4	18.5	35	3.11
7	2	3	2	.	.	.	.	.	.	.	.
8	2	3	2	46.9	26.0	28.0	29.7	3	16.0	21	1.64
9	2	3	2	41.7	34.3	32.5	33.4	3	18.0	24	2.37
10	2	3	2	45.8	35.0	29.0	31.6	3	17.0	25	2.98
1	2	3	3	38.9	34.6	24.0	33.4	2	13.0	25	1.52
2	2	3	3	43.0	40.3	39.2	37.9	2	17.0	27	1.36
3	2	3	3	47.6	30.3	26.7	31.2	2	17.0	23	1.98
4	2	3	3	32.5	24.6	23.5	26.4	3	14.5	21	1.87
5	2	3	3	40.9	31.8	22.2	30.5	3	16.5	20	2.08
6	2	3	3	41.1	31.4	27.4	28.6	3	15.0	22	2.53
7	2	3	3	.	.	.	.	.	.	.	.
8	2	3	3	27.8	25.7	26.4	33.0	2	18.0	23	1.34
9	2	3	3	48.0	40.0	29.0	37.6	3	15.0	25	2.36
10	2	3	3	40.0	29.9	26.5	33.4	3	14.0	24	2.15
1	2	3	4	45.0	39.5	38.0	31.9	1	14.0	20	0.54
2	2	3	4	43.4	32.4	30.0	23.3	1	17.0	22	0.59
3	2	3	4	44.0	34.6	26.4	22.5	3	18.0	23	1.38
4	2	3	4	37.0	26.5	26.0	25.4	2	16.0	19	0.87
5	2	3	4	43.3	20.4	26.7	25.7	2	16.0	20	1.11
6	2	3	4	38.0	34.1	34.1	27.4	3	15.0	22	2.04
7	2	3	4	.	.	.	.	.	.	.	.
8	2	3	4	33.5	23.6	20.0	18.0	1	17.5	19	0.59
9	2	3	4	40.1	29.6	29.7	28.9	2	15.0	17	0.94
10	2	3	4	47.4	29.7	22.0	18.0	1	13.0	15	0.69

APPENDIX 2

DATA OF YIELD LOSS STUDY EXPERIMENT

ENT	YR	REP	TRT	CHL	HGT	YLD
1	1	1	1	40.4	23.3	0.153
1	1	1	2	47.9	23.0	0.153
1	1	2	1	39.3	24.3	0.165
1	1	2	2	48.0	22.3	0.213
2	1	1	1	33.2	25.7	0.134
2	1	1	2	39.1	28.0	0.341
2	1	2	1	36.0	24.7	0.165
2	1	2	2	40.5	28.7	0.306
3	1	1	1	36.4	21.0	0.191
3	1	1	2	39.0	25.7	0.185
3	1	2	1	40.6	22.7	0.208
3	1	2	2	42.9	25.0	0.228
4	1	1	1	39.2	24.0	0.211
4	1	1	2	47.6	24.7	0.241
4	1	2	1	38.2	23.7	0.170
4	1	2	2	39.6	25.2	0.320
5	1	1	1	34.0	21.7	0.111
5	1	1	2	36.6	25.7	0.300
5	1	2	1	37.3	22.7	0.151
5	1	2	2	48.4	25.7	0.255
6	1	1	1	38.4	25.7	0.140
6	1	1	2	44.0	31.7	0.211
6	1	2	1	32.5	24.7	0.120
6	1	2	2	43.0	27.7	0.149
7	1	1	1	29.0	24.0	0.216
7	1	1	2	41.0	27.3	0.324
7	1	2	1	33.0	24.3	0.200
7	1	2	2	39.6	26.3	0.248
8	1	1	1	36.8	29.0	0.165
8	1	1	2	41.6	33.8	0.269
8	1	2	1	35.3	29.7	0.185
8	1	2	2	42.0	33.0	0.266
9	1	1	1	41.9	24.3	0.184
9	1	1	2	47.9	28.2	0.251
9	1	2	1	36.0	26.0	0.165
9	1	2	2	45.9	29.3	0.270
10	1	1	1	39.5	23.0	0.148
10	1	1	2	48.2	27.3	0.250
10	1	2	1	37.6	25.3	0.168
10	1	2	2	44.9	26.7	0.233

ENT	YR	REP	TRT	CHL	HGT	KERNEL	KERN.WGT	YLD
11	1	1	1	40.6	26.7	.	.	0.236
11	1	1	2	46.2	28.7	.	.	0.263
11	1	2	1	40.6	28.7	.	.	0.222
11	1	2	2	49.0	28.7	.	.	0.299
12	1	1	1	37.3	23.7	.	.	0.200
12	1	1	2	40.2	31.3	.	.	0.294
12	1	2	1	36.4	26.7	.	.	0.162
12	1	2	2	42.3	29.7	.	.	0.246
13	1	1	1	46.1	23.7	.	.	0.167
13	1	1	2	49.2	28.7	.	.	0.206
13	1	2	1	35.0	24.7	.	.	0.178
13	1	2	2	44.9	26.7	.	.	0.241
14	1	1	1	33.5	25.0	.	.	0.186
14	1	1	2	40.9	27.3	.	.	0.248
14	1	2	1	35.2	24.0	.	.	0.220
14	1	2	2	39.5	28.3	.	.	0.279
15	1	1	1	35.5	25.3	.	.	0.142
15	1	1	2	39.1	29.0	.	.	0.279
15	1	2	1	37.9	25.8	.	.	0.187
15	1	2	2	42.0	29.0	.	.	0.309
1	2	1	1	38.0	28.0	39	3.23	0.388
1	2	1	2	48.5	29.0	47	3.46	0.509
1	2	2	1	34.1	29.0	43	3.34	0.353
1	2	2	2	46.6	28.0	48	3.28	0.530
1	2	3	1	39.1	31.0	42	3.15	0.425
1	2	3	2	45.3	31.0	44	3.43	0.554
2	2	1	1	44.7	36.0	42	3.68	0.414
2	2	1	2	46.8	40.0	49	3.82	0.618
2	2	2	1	39.2	36.0	44	3.30	0.533
2	2	2	2	45.0	41.0	46	3.93	0.653
2	2	3	1	38.2	36.0	44	3.84	0.522
2	2	3	2	48.8	40.0	50	3.70	0.667
3	2	1	1	41.1	32.0	28	4.14	0.387
3	2	1	2	48.5	36.0	33	4.06	0.591
3	2	2	1	36.4	33.0	31	4.15	0.476
3	2	2	2	46.8	36.0	33	3.90	0.621
3	2	3	1	41.2	32.0	29	3.84	0.426
3	2	3	2	43.9	35.0	37	3.86	0.564
4	2	1	1	35.5	32.0	36	3.76	0.292
4	2	1	2	45.0	34.0	39	3.84	0.533
4	2	2	1	41.8	30.0	34	3.44	0.292
4	2	2	2	45.2	38.0	38	3.73	0.551
4	2	3	1	40.5	28.0	36	3.39	0.285
4	2	3	2	45.8	35.0	39	3.63	0.546
5	2	1	1	35.8	33.0	26	3.33	0.308
5	2	1	2	44.3	37.0	39	3.67	0.650
5	2	2	1	40.1	34.0	28	3.20	0.325
5	2	2	2	45.3	40.0	39	3.77	0.561
5	2	3	1	38.8	31.0	29	3.45	0.260
5	2	3	2	43.2	35.0	38	3.50	0.741

ENT	YR	REP	TRT	CHL	HGT	KERNEL	KERN.WGT	YLD
6	2	1	1	30.3	30.0	35	3.19	0.442
6	2	1	2	41.9	35.0	33	3.39	0.475
6	2	2	1	36.1	30.0	38	3.36	0.398
6	2	2	2	42.3	34.0	39	3.44	0.414
6	2	3	1	40.3	34.0	37	3.44	0.421
6	2	3	2	44.2	38.0	35	3.19	0.393
7	2	1	1	42.0	32.0	44	3.32	0.500
7	2	1	2	49.6	35.0	43	3.57	0.716
7	2	2	1	36.4	35.0	42	3.42	0.566
7	2	2	2	49.6	36.0	43	3.49	0.806
7	2	3	1	37.0	36.0	40	3.24	0.593
7	2	3	2	46.0	35.0	47	3.58	0.711
8	2	1	1	35.0	34.0	23	3.62	0.252
8	2	1	2	43.5	40.0	39	3.93	0.731
8	2	2	1	35.1	32.0	30	3.75	0.253
8	2	2	2	44.0	42.0	39	3.84	0.695
8	2	3	1	40.5	31.0	28	3.39	0.256
8	2	3	2	44.4	39.0	41	3.68	0.733
9	2	1	1	36.9	35.0	34	3.83	0.337
9	2	1	2	47.0	39.0	39	4.08	0.793
9	2	2	1	38.8	36.0	33	3.64	0.332
9	2	2	2	47.7	40.0	42	3.99	0.749
9	2	3	1	41.7	37.0	36	3.67	0.307
9	2	3	2	48.0	38.0	39	3.83	0.630
10	2	1	1	36.7	32.0	28	3.86	0.413
10	2	1	2	48.8	34.0	35	3.96	0.582
10	2	2	1	40.1	32.0	30	4.04	0.398
10	2	2	2	46.3	35.0	40	3.94	0.615
10	2	3	1	37.8	33.0	30	3.95	0.593
10	2	3	2	47.4	34.0	35	3.83	0.681
11	2	1	1	41.0	36.0	33	4.26	0.302
11	2	1	2	42.9	41.0	38	4.54	0.591
11	2	2	1	41.0	38.0	34	4.16	0.336
11	2	2	2	46.5	40.0	36	4.47	0.907
11	2	3	1	45.0	37.0	37	4.40	0.306
11	2	3	2	49.3	42.0	41	4.52	0.629
12	2	1	1	36.3	34.0	38	3.61	0.295
12	2	1	2	45.5	37.0	43	4.10	0.646
12	2	2	1	35.8	35.0	40	3.76	0.295
12	2	2	2	43.3	38.0	48	4.22	0.622
12	2	3	1	40.1	37.0	43	4.04	0.437
12	2	3	2	43.7	38.0	50	3.94	0.617
13	2	1	1	33.0	26.0	29	3.46	0.264
13	2	1	2	49.8	32.0	40	3.46	0.665
13	2	2	1	43.0	28.0	28	3.26	0.228
13	2	2	2	48.0	34.0	40	3.71	0.718
13	2	3	1	40.8	28.0	28	3.34	0.120
13	2	3	2	48.0	36.0	39	3.69	0.758
14	2	1	1	37.8	34.0	33	3.03	0.364
14	2	1	2	48.0	35.0	33	3.01	0.676
14	2	2	1	35.9	32.0	31	2.92	0.305

ENT	YR	REP	TRT	CHL	HGT	TILLER	KERNEL	KERN.WGT	YLD
14	2	2	2	47.0	37.0	.	35	2.96	0.597
14	2	3	1	38.4	35.0	.	35	2.87	0.319
14	2	3	2	48.0	35.0	.	34	2.80	0.655
15	2	1	1	29.8	29.0	.	42	2.68	0.271
15	2	1	2	45.0	31.0	.	40	2.56	0.319
15	2	2	1	31.0	31.0	.	44	2.66	0.299
15	2	2	2	42.0	34.0	.	39	2.70	0.414
15	2	3	1	33.4	32.0	.	41	2.82	0.419
15	2	3	2	44.3	34.0	.	43	2.65	0.450
1	3	1	1	28.2	22.0	13	29	2.46	0.185
1	3	1	2	40.1	23.0	24	33	2.76	0.269
1	3	2	1	30.2	24.0	18	28	2.52	0.134
1	3	2	2	41.7	25.0	31	37	2.96	0.323
1	3	3	1	31.8	22.0	18	32	3.15	0.255
1	3	3	2	37.8	23.0	25	37	3.46	0.320
2	3	1	1	36.8	25.5	21	31	3.59	0.330
2	3	1	2	47.1	26.0	32	41	3.98	0.556
2	3	2	1	34.5	24.0	12	21	3.21	0.316
2	3	2	2	47.4	28.0	22	34	3.77	0.538
2	3	3	1	33.4	27.0	20	28	3.70	0.396
2	3	3	2	48.4	31.0	27	40	4.05	0.621
3	3	1	1	36.5	24.0	19	22	3.88	0.288
3	3	1	2	44.9	27.0	38	33	4.04	0.473
3	3	2	1	37.4	22.0	20	27	3.82	0.242
3	3	2	2	42.6	28.0	30	33	4.20	0.593
3	3	3	1	30.5	23.5	16	24	3.89	0.303
3	3	3	2	44.6	29.0	41	29	4.18	0.636
4	3	1	1	43.0	25.0	19	28	3.66	0.284
4	3	1	2	45.4	25.5	38	47	3.98	0.623
4	3	2	1	37.2	22.5	17	27	3.23	0.282
4	3	2	2	44.0	26.5	34	50	3.84	0.590
4	3	3	1	33.0	24.0	16	26	3.56	0.281
4	3	3	2	45.4	28.0	31	49	3.69	0.623
5	3	1	1	33.0	23.0	16	27	3.23	0.248
5	3	1	2	43.0	31.5	36	39	3.43	0.549
5	3	2	1	34.2	26.0	18	29	3.61	0.314
5	3	2	2	42.8	30.5	34	37	4.01	0.653
5	3	3	1	30.9	24.0	19	25	3.41	0.267
5	3	3	2	40.7	31.0	27	33	3.66	0.511
6	3	1	1	33.5	23.0	11	28	3.41	0.154
6	3	1	2	43.5	24.0	18	34	3.25	0.232
6	3	2	1	27.0	24.0	12	30	2.88	0.162
6	3	2	2	39.1	25.0	21	36	3.60	0.236
6	3	3	1	21.4	24.0	13	29	3.58	0.167
6	3	3	2	42.7	28.0	19	33	3.68	0.229
7	3	1	1	36.4	23.0	16	26	2.66	0.253
7	3	1	2	42.0	32.0	28	43	4.51	0.627
7	3	2	1	27.0	22.0	21	28	2.95	0.221
7	3	2	2	43.5	30.0	32	39	3.60	0.633
7	3	3	1	32.5	26.5	21	18	3.14	0.272
7	3	3	2	39.5	29.0	32	41	3.47	0.589

ENT	YR	REP	TRT	CHL	HGT	TILLER	KERNEL	KERN.WGT	YLD
8	3	1	1	33.6	27.0	14	25	3.71	0.320
8	3	1	2	42.2	31.0	32	39	3.98	0.645
8	3	2	1	28.0	25.0	12	20	3.54	0.230
8	3	2	2	37.0	33.5	31	32	3.78	0.621
8	3	3	1	25.7	25.0	18	22	3.56	0.273
8	3	3	2	42.1	36.0	38	37	4.59	0.665
9	3	1	1	38.9	24.0	16	25	3.79	0.287
9	3	1	2	47.4	33.0	33	33	4.03	0.656
9	3	2	1	33.8	26.0	14	23	3.91	0.265
9	3	2	2	43.3	30.0	37	40	4.26	0.671
9	3	3	1	35.2	27.0	27	22	3.81	0.301
9	3	3	2	39.3	33.0	34	31	4.34	0.554
10	3	1	1	35.2	26.5	19	28	3.56	0.324
10	3	1	2	44.0	24.5	37	32	3.95	0.554
10	3	2	1	37.7	24.0	12	23	3.70	0.259
10	3	2	2	48.0	26.5	27	31	3.93	0.492
10	3	3	1	36.9	24.0	20	24	3.89	0.362
10	3	3	2	44.2	28.5	37	33	4.01	0.572
11	3	1	1	36.1	27.5	12	26	4.27	0.332
11	3	1	2	46.7	29.5	30	42	4.94	0.650
11	3	2	1	38.1	22.0	13	24	4.10	0.290
11	3	2	2	48.1	29.5	24	41	4.96	0.584
11	3	3	1	35.7	24.0	16	25	4.15	0.311
11	3	3	2	43.1	31.0	30	46	4.70	0.616
12	3	1	1	35.3	27.0	12	28	3.78	0.297
12	3	1	2	45.0	29.0	30	42	4.16	0.531
12	3	2	1	32.2	25.0	10	26	3.76	0.271
12	3	2	2	40.0	29.5	32	39	4.06	0.743
12	3	3	1	31.4	25.0	18	24	3.56	0.331
12	3	3	2	38.1	30.0	34	44	4.41	0.535
13	3	1	1	36.3	20.0	17	20	3.12	0.246
13	3	1	2	43.8	28.5	28	31	3.87	0.590
13	3	2	1	33.0	21.0	17	24	3.24	0.239
13	3	2	2	44.7	28.5	30	31	4.08	0.550
13	3	3	1	36.4	22.0	12	25	3.25	0.227
13	3	3	2	45.3	28.0	32	34	3.68	0.639
14	3	1	1	36.4	23.5	23	29	2.96	0.286
14	3	1	2	44.5	31.0	39	33	3.12	0.548
14	3	2	1	33.0	23.0	22	31	2.86	0.283
14	3	2	2	41.9	29.0	33	35	3.12	0.567
14	3	3	1	31.6	26.0	26	29	2.87	0.277
14	3	3	2	41.1	32.0	37	37	3.02	0.595
15	3	1	1	23.0	21.5	18	27	2.71	0.192
15	3	1	2	41.0	26.0	20	33	2.98	0.255
15	3	2	1	24.0	22.0	22	29	2.63	0.214
15	3	2	2	42.0	27.0	22	35	3.46	0.283
15	3	3	1	26.2	22.5	20	26	2.83	0.219
15	3	3	2	41.2	28.5	23	37	3.40	0.293

APPENDIX 3

DATA OF HERITABILITY EXPERIMENT

ENT	YR	REP	CHL	HGT	YLD
1	1	1	34.5	25.3	150.0
1	1	2	31.6	22.0	130.0
1	1	3	35.2	24.7	141.3
2	1	1	34.5	24.2	178.0
2	1	2	36.0	24.0	172.6
2	1	3	37.0	25.0	167.0
3	1	1	34.0	26.0	148.0
3	1	2	32.4	25.7	120.0
3	1	3	31.8	25.3	.
4	1	1	33.0	27.7	108.5
4	1	2	33.3	28.0	113.0
4	1	3	32.3	26.7	123.0
5	1	1	30.5	19.3	89.0
5	1	2	34.8	21.3	90.0
5	1	3	35.3	21.0	92.0
6	1	1	33.5	25.0	79.0
6	1	2	33.8	25.0	82.0
6	1	3	36.8	23.7	61.0
7	1	1	33.8	25.0	109.0
7	1	2	32.0	26.3	137.0
7	1	3	33.5	24.3	.
8	1	1	34.2	22.0	60.0
8	1	2	33.5	19.3	50.0
8	1	3	33.7	20.3	44.0
9	1	1	36.6	25.3	142.0
9	1	2	36.0	23.7	108.0
9	1	3	34.4	23.7	98.0
10	1	1	29.8	23.7	110.0
10	1	2	26.1	21.7	107.0
10	1	3	28.3	24.0	.
11	1	1	30.5	27.3	123.0
11	1	2	32.2	27.7	87.0
11	1	3	33.9	26.0	84.0
12	1	1	37.0	24.0	145.5
12	1	2	34.7	21.3	132.0
12	1	3	37.5	20.7	.
13	1	1	38.0	22.7	50.0
13	1	2	41.2	24.0	47.0
13	1	3	36.3	22.7	62.0
14	1	1	38.2	21.3	114.0
14	1	2	41.9	23.3	128.2
14	1	3	38.8	21.0	.

ENT	YR	REP	CHL	HGT	YLD
15	1	1	36.2	23.3	120.0
15	1	2	37.0	22.0	112.0
15	1	3	38.3	19.7	101.7
16	1	1	37.5	23.0	128.0
16	1	2	39.9	20.0	90.6
16	1	3	35.8	18.3	86.2
17	1	1	32.4	25.3	156.0
17	1	2	32.1	26.7	136.0
17	1	3	29.3	26.3	.
18	1	1	34.3	26.3	107.0
18	1	2	38.2	27.3	101.0
18	1	3	37.7	24.7	120.0
19	1	1	33.6	26.7	126.0
19	1	2	33.9	28.0	101.0
19	1	3	31.4	25.7	.
20	1	1	34.9	23.8	134.0
20	1	2	35.0	22.0	117.0
20	1	3	32.5	20.3	.
21	1	1	32.1	23.7	93.8
21	1	2	42.9	22.0	121.5
21	1	3	37.6	21.3	86.0
22	1	1	36.8	24.3	113.0
22	1	2	37.9	22.7	107.0
22	1	3	37.5	21.0	.
23	1	1	28.0	19.7	113.0
23	1	2	23.8	21.7	111.4
23	1	3	29.1	20.3	109.8
24	1	1	38.3	20.7	68.0
24	1	2	34.7	20.7	47.0
24	1	3	36.0	20.0	56.0
25	1	1	40.5	24.8	100.0
25	1	2	39.9	21.0	68.0
25	1	3	38.7	19.0	94.0
26	1	1	38.8	25.3	141.0
26	1	2	35.0	22.0	124.0
26	1	3	37.8	21.0	111.8
27	1	1	39.2	21.0	117.0
27	1	2	38.1	18.3	94.3
27	1	3	41.1	21.7	.
28	1	1	34.4	26.0	92.0
28	1	2	32.6	24.3	87.0
28	1	3	31.8	23.7	.
29	1	1	32.3	22.3	106.0
29	1	2	32.0	21.3	111.0
29	1	3	31.3	19.7	154.4

ENT	YR	REP	CHL	HGT	YLD
30	1	1	33.6	25.0	83.0
30	1	2	34.3	26.3	87.0
30	1	3	35.6	25.0	108.0
31	1	1	31.6	21.0	93.0
31	1	2	35.5	21.3	121.0
31	1	3	34.0	21.0	97.0
32	1	1	39.0	25.7	205.3
32	1	2	38.3	25.3	168.0
32	1	3	.	.	.
33	1	1	37.9	31.3	162.0
33	1	2	44.8	26.7	95.0
33	1	3	36.7	26.0	106.0
34	1	1	33.7	24.5	114.0
34	1	2	33.1	22.7	144.6
34	1	3	35.2	22.3	106.0
35	1	1	31.0	26.0	67.9
35	1	2	30.0	23.7	57.3
35	1	3	31.4	24.7	58.0
36	1	1	33.7	21.0	114.0
36	1	2	33.3	24.3	98.0
36	1	3	32.7	22.7	130.0
37	1	1	33.7	24.3	127.0
37	1	2	31.2	22.0	93.0
37	1	3	30.3	24.0	86.0
38	1	1	40.3	29.3	136.0
38	1	2	36.8	27.7	136.6
38	1	3	30.8	27.3	103.0
39	1	1	39.1	22.7	141.0
39	1	2	36.2	22.3	113.0
39	1	3	38.7	24.0	124.0
40	1	1	32.3	26.0	144.0
40	1	2	32.0	26.0	122.0
40	1	3	34.7	25.7	.
41	1	1	32.7	26.0	159.0
41	1	2	32.7	24.3	151.3
41	1	3	34.7	23.3	.
42	1	1	35.1	24.3	172.0
42	1	2	32.3	21.3	139.0
42	1	3	34.0	23.0	.
43	1	1	37.0	22.0	127.0
43	1	2	.	.	.
43	1	3	34.5	19.7	92.0
44	1	1	39.9	22.3	109.0
44	1	2	37.3	24.0	138.0
44	1	3	33.8	20.7	119.2

ENT	YR	REP	CHL	HGT	YLD
45	1	1	36.0	27.5	159.0
45	1	2	38.0	26.3	152.0
45	1	3	37.8	25.7	137.0
46	1	1	34.8	24.7	92.0
46	1	2	40.0	24.7	122.0
46	1	3	35.3	23.7	.
47	1	1	29.0	25.0	131.0
47	1	2	33.3	25.7	126.0
47	1	3	30.0	23.7	.
48	1	1	34.7	25.0	78.0
48	1	2	37.9	28.3	100.0
48	1	3	35.7	24.3	83.0
49	1	1	32.7	26.3	121.0
49	1	2	33.8	25.3	125.7
49	1	3	36.4	24.3	134.3
50	1	1	43.1	21.7	134.0
50	1	2	44.9	23.0	131.2
50	1	3	42.5	20.7	.
51	1	1	36.4	23.3	68.0
51	1	2	37.0	23.0	54.0
51	1	3	37.5	25.3	69.0
52	1	1	34.2	25.0	148.0
52	1	2	37.0	23.0	156.0
52	1	3	33.4	20.0	.
53	1	1	36.8	24.0	142.0
53	1	2	37.7	23.3	94.0
53	1	3	38.3	18.3	96.0
54	1	1	34.0	24.3	.
54	1	2	30.5	23.7	134.0
54	1	3	31.1	25.0	138.0
55	1	1	36.0	25.3	130.0
55	1	2	35.9	26.0	108.0
55	1	3	38.5	23.3	.
56	1	1	38.3	29.7	135.0
56	1	2	40.1	31.0	142.0
56	1	3	41.3	29.3	166.3
57	1	1	32.6	28.3	190.0
57	1	2	36.2	25.7	187.0
57	1	3	37.6	26.0	212.3
58	1	1	36.5	21.3	62.0
58	1	2	36.1	23.7	78.0
58	1	3	32.4	22.7	.
59	1	1	32.2	20.0	49.0
59	1	2	33.2	19.3	47.0
59	1	3	35.5	21.7	64.0

ENT	YR	REP	CHL	HGT	YLD
60	1	1	36.8	29.3	.
60	1	2	35.9	27.3	144.0
60	1	3	35.7	29.3	180.6
61	1	1	34.3	27.2	152.6
61	1	2	33.4	33.7	147.0
61	1	3	35.6	27.0	.
62	1	1	32.0	28.7	134.0
62	1	2	33.2	28.3	184.3
62	1	3	31.9	27.0	125.0
63	1	1	30.9	24.2	134.0
63	1	2	29.4	26.7	146.3
63	1	3	28.0	26.3	186.4
64	1	1	31.3	26.7	107.0
64	1	2	34.3	25.0	90.0
64	1	3	34.0	25.3	124.0
65	1	1	32.4	22.0	77.0
65	1	2	.	23.0	113.0
65	1	3	31.5	20.3	96.7
66	1	1	30.5	29.0	123.0
66	1	2	33.0	32.0	133.0
66	1	3	32.4	30.3	121.3
67	1	1	34.1	27.3	115.0
67	1	2	35.6	25.3	.
67	1	3	34.1	27.3	105.0
68	1	1	30.8	20.7	66.1
68	1	2	.	.	.
68	1	3	34.4	21.0	49.0
69	1	1	36.0	22.7	126.0
69	1	2	34.8	22.3	133.9
69	1	3	38.1	19.7	120.0
70	1	1	37.8	26.0	92.8
70	1	2	34.7	25.0	109.5
70	1	3	.	.	.
71	1	1	33.0	30.8	129.0
71	1	2	38.2	29.0	98.0
71	1	3	37.1	24.3	112.0
72	1	1	33.7	25.7	134.0
72	1	2	35.2	25.7	113.0
72	1	3	34.5	23.3	118.0
73	1	1	33.0	25.7	110.0
73	1	2	32.3	23.0	126.1
73	1	3	34.1	22.7	105.0
74	1	1	34.9	27.0	116.0
74	1	2	36.4	29.3	109.0
74	1	3	32.0	26.7	95.0

ENT	YR	REP	CHL	HGT	KERNEL	KERNEL WGT	YLD
75	1	1	29.6	25.3	.	.	116.0
75	1	2	34.2	25.3	.	.	115.0
75	1	3	34.0	26.3	.	.	144.8
76	1	1	33.9	24.3	.	.	144.7
76	1	2	34.0	22.7	.	.	147.6
76	1	3	30.0	22.0	.	.	.
77	1	1	33.0	26.0	.	.	131.0
77	1	2	35.4	24.0	.	.	129.0
77	1	3	34.5	24.3	.	.	.
78	1	1	34.6	23.2	.	.	128.8
78	1	2	33.9	22.3	.	.	113.0
78	1	3	36.6	22.3	.	.	120.0
79	1	1	32.7	29.3	.	.	151.8
79	1	2	33.0	29.3	.	.	160.0
79	1	3	33.0	28.0	.	.	138.0
80	1	1	31.1	29.3	.	.	137.1
80	1	2	34.6	26.3	.	.	122.0
80	1	3	34.2	27.3	.	.	.
1	2	1	39.3	39.0	36	3.00	118.6
1	2	2	40.4	38.0	30	3.00	98.2
1	2	3	40.7	40.0	32	2.98	108.9
2	2	1	40.8	41.0	39	3.48	80.9
2	2	2	40.9	42.5	38	3.31	119.5
2	2	3	38.0	41.0	36	3.21	76.0
3	2	1	31.2	32.0	35	3.43	112.6
3	2	2	37.8	32.0	30	3.79	96.5
3	2	3	37.0	32.0	29	3.35	99.3
4	2	1	40.0	41.0	32	3.05	80.3
4	2	2	37.8	41.0	29	3.27	73.2
4	2	3	40.9	40.0	31	3.32	72.2
5	2	1	35.2	39.0	34	3.15	65.3
5	2	2	34.5	41.0	40	3.00	54.3
5	2	3	32.2	39.0	34	3.17	58.4
6	2	1	35.5	42.5	38	3.01	110.2
6	2	2	37.8	41.0	42	2.87	128.1
6	2	3	37.5	40.0	45	3.12	115.9
7	2	1	35.7	35.0	39	3.05	68.9
7	2	2	33.7	32.0	40	2.57	62.4
7	2	3	33.5	36.0	35	3.07	53.6
8	2	1	35.0	44.0	30	2.82	56.3
8	2	2	35.0	43.0	32	3.16	73.3
8	2	3	36.0	42.0	33	2.98	78.3
9	2	1	44.9	35.0	39	3.95	100.4
9	2	2	38.6	36.0	34	3.63	91.3
9	2	3	38.1	36.5	35	3.74	88.9

ENT	YR	REP	CHL	HGT	KERNEL	KERNEL WGT	YLD
10	2	1	32.1	31.0	38	2.75	75.5
10	2	2	38.3	33.5	38	2.75	72.1
10	2	3	35.8	33.0	39	2.89	.
11	2	1	32.8	34.0	33	3.57	71.3
11	2	2	29.9	35.0	38	3.69	88.8
11	2	3	30.0	36.0	33	3.64	69.2
12	2	1	40.0	36.0	35	3.28	127.3
12	2	2	38.0	38.0	31	3.34	105.2
12	2	3	40.6	36.0	32	3.12	115.1
13	2	1	32.3	32.0	29	2.93	60.7
13	2	2	38.6	31.0	32	2.75	48.4
13	2	3	32.0	34.0	31	2.65	42.0
14	2	1	43.4	38.5	40	3.10	100.0
14	2	2	33.6	42.0	30	3.33	105.3
14	2	3	41.3	42.0	37	2.97	104.8
15	2	1	38.2	40.0	38	3.63	96.0
15	2	2	36.8	40.0	40	3.40	77.1
15	2	3	38.8	39.0	33	3.30	89.0
16	2	1	38.9	32.0	36	3.31	95.1
16	2	2	39.0	35.0	30	3.43	62.3
16	2	3	39.0	34.0	32	3.33	84.8
17	2	1	33.8	35.0	31	3.45	90.8
17	2	2	32.6	37.0	31	3.85	114.3
17	2	3	35.7	39.0	34	3.35	99.7
18	2	1	37.0	38.0	31	3.17	97.1
18	2	2	36.0	39.0	36	3.28	94.0
18	2	3	40.0	36.0	35	3.42	119.9
19	2	1	43.3	36.0	27	3.23	152.1
19	2	2	44.5	39.5	22	3.26	116.0
19	2	3	41.3	37.0	29	3.85	.
20	2	1	36.4	42.0	40	3.62	66.0
20	2	2	35.7	40.0	37	3.26	82.7
20	2	3	37.0	40.5	40	3.56	89.4
21	2	1	34.0	29.0	31	2.70	61.7
21	2	2	36.6	32.0	27	3.17	81.3
21	2	3	37.2	30.5	24	3.14	66.0
22	2	1	36.4	35.0	30	3.63	65.5
22	2	2	38.0	36.0	28	3.94	95.8
22	2	3	36.4	36.0	33	3.46	88.2
23	2	1	30.2	31.5	32	3.00	.
23	2	2	34.7	30.0	37	3.43	103.0
23	2	3	38.3	31.0	35	3.23	103.9
24	2	1	35.0	33.0	34	3.87	60.3
24	2	2	35.9	35.0	32	3.84	79.8
24	2	3	33.7	35.0	31	3.88	70.2

ENT	YR	REP	CHL	HGT	KERNEL	KERNEL WGT	YLD
25	2	1	33.5	34.0	28	3.50	137.8
25	2	2	33.4	38.0	35	3.65	128.4
25	2	3	33.7	35.0	34	3.49	.
26	2	1	27.4	37.0	22	3.74	79.6
26	2	2	32.2	34.0	21	3.30	86.0
26	2	3	31.4	37.5	25	3.26	70.9
27	2	1	43.1	38.0	30	3.79	113.8
27	2	2	41.1	37.5	24	3.87	104.8
27	2	3	43.0	36.0	28	3.90	99.5
28	2	1	42.3	31.5	33	2.84	74.5
28	2	2	33.9	31.0	32	3.08	83.2
28	2	3	35.3	28.0	34	2.91	69.0
29	2	1	30.2	32.0	24	3.54	26.8
29	2	2	34.0	30.0	20	3.10	35.0
29	2	3	34.0	32.0	24	3.28	15.5
30	2	1	30.0	32.0	31	3.00	97.9
30	2	2	32.4	32.0	34	3.33	91.7
30	2	3	30.9	28.5	30	2.85	80.5
31	2	1	36.8	31.0	23	3.64	88.6
31	2	2	37.5	34.0	28	3.75	83.6
31	2	3	37.3	32.0	27	3.62	90.3
32	2	1	31.2	36.5	26	2.96	80.1
32	2	2	32.1	35.0	31	2.51	75.2
32	2	3	28.7	36.0	22	3.05	.
33	2	1	32.5	39.0	42	3.74	105.8
33	2	2	33.9	43.0	36	3.69	112.3
33	2	3	36.7	40.0	37	3.88	147.7
34	2	1	40.8	34.0	34	3.06	96.8
34	2	2	40.7	33.0	33	3.21	108.9
34	2	3	41.0	36.0	33	3.13	89.2
35	2	1	34.6	32.0	30	2.88	75.4
35	2	2	35.0	33.0	31	3.17	72.1
35	2	3	32.2	32.0	27	2.78	84.7
36	2	1	31.9	32.0	27	3.44	59.4
36	2	2	31.3	35.0	31	3.68	49.6
36	2	3	32.0	34.0	31	3.45	76.6
37	2	1	32.3	35.0	30	3.53	104.8
37	2	2	34.8	35.0	27	3.80	109.1
37	2	3	34.4	37.0	24	3.49	106.0
38	2	1	35.3	40.0	36	3.04	109.3
38	2	2	33.2	37.0	38	2.91	92.7
38	2	3	34.5	36.0	33	2.77	128.3
39	2	1	38.0	30.0	24	3.47	124.3
39	2	2	35.3	31.0	27	3.41	104.3
39	2	3	35.3	32.0	25	3.19	108.3

ENT	YR	REP	CHL	HGT	KERNEL	KERNEL WGT	YLD
40	2	1	31.5	35.5	33	2.94	84.9
40	2	2	30.9	38.0	27	3.02	70.0
40	2	3	33.1	35.0	28	3.35	85.0
41	2	1	38.8	33.0	30	3.01	82.5
41	2	2	41.4	35.0	33	2.86	74.3
41	2	3	40.9	34.0	26	2.80	78.5
42	2	1	40.7	38.0	27	3.82	132.4
42	2	2	40.8	37.5	36	3.95	128.7
42	2	3	44.1	35.0	37	3.73	116.1
43	2	1	34.5	36.0	27	3.70	87.0
43	2	2	34.3	33.0	27	3.46	88.9
43	2	3	35.3	33.0	24	3.56	61.8
44	2	1	34.8	38.0	26	3.97	121.9
44	2	2	36.7	36.5	25	4.30	98.4
44	2	3	36.9	34.5	25	4.16	112.3
45	2	1	35.1	32.0	37	2.87	84.7
45	2	2	38.3	33.0	41	3.20	105.0
45	2	3	41.3	29.0	37	2.71	98.2
46	2	1	41.5	34.0	39	3.36	122.7
46	2	2	42.0	33.0	32	3.20	106.5
46	2	3	46.2	32.0	30	3.40	123.4
47	2	1	37.9	36.0	43	3.80	157.9
47	2	2	37.2	39.0	40	3.98	119.3
47	2	3	38.5	36.0	43	3.56	.
48	2	1	38.0	42.0	27	3.73	80.4
48	2	2	38.3	40.5	23	3.94	84.6
48	2	3	38.7	39.0	25	3.69	101.5
49	2	1	42.6	42.0	36	3.62	84.1
49	2	2	38.0	38.0	32	3.41	91.9
49	2	3	39.0	39.0	33	3.62	83.9
50	2	1	42.1	33.0	32	3.83	117.3
50	2	2	38.0	34.0	26	4.18	118.5
50	2	3	42.7	35.0	33	3.72	110.5
51	2	1	34.0	39.0	29	3.60	86.5
51	2	2	36.4	36.0	35	3.75	93.0
51	2	3	36.9	36.0	30	3.60	85.6
52	2	1	38.0	34.0	39	3.62	175.6
52	2	2	39.0	36.0	31	3.52	128.1
52	2	3	42.5	35.0	30	3.91	144.7
53	2	1	32.4	36.0	28	4.04	90.1
53	2	2	35.6	38.5	30	3.90	104.7
53	2	3	34.6	37.0	32	3.86	88.8

ENT	YR	REP	CHL	HGT	KERNEL	KERNEL WGT	YLD
54	2	1	33.8	32.0	25	3.55	35.5
54	2	2	32.8	33.0	22	3.83	53.7
54	2	3	34.4	32.0	24	3.66	50.5
55	2	1	36.1	38.0	34	3.39	.
55	2	2	33.8	41.0	31	3.27	134.9
55	2	3	34.8	39.0	32	3.37	108.1
56	2	1	35.0	40.5	28	4.32	81.8
56	2	2	33.3	42.0	33	3.64	77.5
56	2	3	36.0	38.0	26	3.80	87.9
57	2	1	33.2	38.5	40	3.44	137.2
57	2	2	31.0	41.0	38	3.45	127.3
57	2	3	35.4	39.0	36	3.19	136.3
58	2	1	39.5	37.0	30	3.10	113.6
58	2	2	36.4	37.0	28	3.30	104.5
58	2	3	35.0	36.0	27	3.40	108.2
59	2	1	42.7	30.0	32	3.80	130.5
59	2	2	38.1	28.0	26	3.45	133.8
59	2	3	40.7	32.0	25	3.70	131.3
60	2	1	30.8	39.0	29	3.64	75.6
60	2	2	34.8	42.0	28	4.03	78.6
60	2	3	34.1	38.0	27	3.83	64.8
61	2	1	37.9	44.0	35	3.81	113.4
61	2	2	38.5	41.0	34	3.47	105.7
61	2	3	36.8	39.0	36	3.83	101.3
62	2	1	39.3	44.0	45	3.52	114.8
62	2	2	41.8	40.0	39	3.90	131.2
62	2	3	37.2	43.0	44	3.47	117.7
63	2	1	29.4	33.0	21	3.65	71.3
63	2	2	28.5	31.0	25	3.68	41.8
63	2	3	31.2	33.0	26	3.51	45.2
64	2	1	32.8	43.0	39	3.50	.
64	2	2	29.7	41.0	42	3.59	100.6
64	2	3	30.1	42.0	39	3.52	115.0
65	2	1	41.2	30.0	36	3.52	129.1
65	2	2	43.5	32.0	35	3.87	113.6
65	2	3	46.9	31.5	37	3.91	139.7
66	2	1	30.9	44.0	35	3.23	137.6
66	2	2	32.6	44.5	32	3.51	101.0
66	2	3	33.5	47.0	34	3.35	109.8
67	2	1	34.8	36.0	26	3.42	70.8
67	2	2	36.0	40.0	31	3.60	81.1
67	2	3	36.5	40.0	34	3.31	89.2
68	2	1	39.7	36.0	39	3.45	99.4
68	2	2	40.8	39.0	38	3.60	107.5
68	2	3	41.0	39.0	41	3.30	93.6

ENT	YR	REP	CHL	HGT	TILLER	KERNEL	KERNEL WGT	YLD
69	2	1	38.9	31.0	.	33	3.06	159.1
69	2	2	38.7	32.0	.	29	3.29	143.4
69	2	3	39.3	31.5	.	33	3.05	133.2
70	2	1	33.6	40.0	.	35	3.43	81.6
70	2	2	32.5	38.0	.	34	3.15	60.9
70	2	3	30.0	37.0	.	35	3.00	55.9
71	2	1	38.5	43.0	.	36	3.54	105.5
71	2	2	38.3	43.5	.	34	3.70	117.0
71	2	3	41.2	45.0	.	35	3.81	100.9
72	2	1	37.2	40.0	.	35	3.25	114.0
72	2	2	34.0	40.0	.	37	3.27	101.7
72	2	3	35.8	42.0	.	38	3.46	95.7
73	2	1	42.3	42.5	.	45	3.00	118.3
73	2	2	41.4	42.0	.	41	3.20	103.5
73	2	3	40.3	44.0	.	43	3.30	93.6
74	2	1	29.0	37.0	.	40	3.25	78.0
74	2	2	34.5	39.0	.	40	3.23	104.0
74	2	3	35.0	40.0	.	39	3.20	90.8
75	2	1	38.4	41.0	.	46	3.39	107.8
75	2	2	35.3	40.0	.	37	3.53	99.2
75	2	3	37.8	41.0	.	38	3.63	111.1
76	2	1	38.0	35.0	.	39	3.71	157.8
76	2	2	35.0	37.0	.	37	3.97	138.0
76	2	3	40.2	35.0	.	42	3.63	117.6
77	2	1	39.0	36.5	.	38	3.28	88.0
77	2	2	38.8	40.0	.	38	3.50	92.0
77	2	3	41.4	36.5	.	44	3.37	118.1
78	2	1	40.8	32.0	.	41	2.85	98.9
78	2	2	41.3	32.0	.	40	3.36	76.4
78	2	3	38.9	28.5	.	39	3.00	86.3
79	2	1	36.0	45.0	.	44	3.20	113.5
79	2	2	36.2	42.0	.	39	3.50	106.5
79	2	3	38.3	48.0	.	38	3.50	95.9
80	2	1	34.6	43.0	.	42	3.55	.
80	2	2	36.7	41.0	.	36	3.58	127.8
80	2	3	37.2	39.0	.	35	3.58	135.2
1	3	1	40.3	24.0	15	23	2.89	74.3
1	3	2	40.0	24.0	14	22	2.91	70.5
1	3	3	41.6	25.0	.	22	2.95	78.7
2	3	1	34.2	22.0	10	24	3.12	23.5
2	3	2	30.7	22.0	8	21	3.06	27.6
2	3	3	35.3	23.0	.	23	3.04	22.5
3	3	1	33.8	22.0	20	24	3.08	37.8
3	3	2	33.1	21.0	20	22	3.02	34.3
3	3	3	33.0	20.0	.	21	2.94	32.1

ENT	YR	REP	CHL	HGT	TILLER	KERNEL	KERNEL WGT	YLD
4	3	1	32.0	25.0	25	25	2.58	42.3
4	3	2	33.9	24.0	25	27	2.66	47.3
4	3	3	35.0	.	.	.	.	.
5	3	1	30.3	23.0	24	21	2.72	43.8
5	3	2	33.1	24.0	20	20	2.92	54.3
5	3	3	32.4	26.0	.	22	2.86	59.0
6	3	1	35.8	.	.	.	.	.
6	3	2	33.9	.	.	.	.	.
6	3	3	31.6	23.5	.	25	3.92	41.2
7	3	1	31.3	24.0	16	28	2.05	40.9
7	3	2	30.0	23.5	18	32	1.96	42.4
7	3	3	20.0	23.0	.	22	2.01	40.3
8	3	1	27.3	22.0	21	21	2.13	35.6
8	3	2	26.9	22.0	20	23	1.96	34.8
8	3	3	25.0	22.0	20	21	1.78	33.6
9	3	1	44.2	26.0	34	27	3.30	96.5
9	3	2	44.1	24.5	30	24	3.52	85.4
9	3	3	.	.	.	.	.	.
10	3	1	28.1	19.5	18	21	2.88	34.0
10	3	2	27.6	19.5	20	21	2.44	36.4
10	3	3	29.2	20.0	.	25	2.71	46.1
11	3	1	31.3	21.0	24	21	2.67	27.1
11	3	2	30.8	19.5	19	18	2.48	27.3
11	3	3	29.9	21.0	.	21	2.22	21.1
12	3	1	27.8	18.0	19	20	2.63	29.8
12	3	2	26.5	20.5	22	19	2.42	30.6
12	3	3	25.8	19.0	.	18	2.38	28.9
13	3	1	32.9	23.0	20	23	2.91	34.8
13	3	2	33.4	23.0	19	19	2.84	34.1
13	3	3	33.5	23.0	.	18	2.72	33.5
14	3	1	36.4	20.0	20	22	2.92	64.4
14	3	2	31.5	19.0	21	18	2.42	51.7
14	3	3	37.4	20.0	.	24	2.61	73.3
15	3	1	32.6	20.0	15	17	3.07	23.6
15	3	2	31.5	21.5	18	18	2.84	30.6
15	3	3	32.3	20.0	.	16	2.94	26.8
16	3	1	37.0	19.0	17	16	2.89	31.0
16	3	2	35.4	21.0	20	19	2.92	41.4
16	3	3	38.6	21.0	.	18	2.86	38.7
17	3	1	29.7	22.5	12	21	3.36	37.6
17	3	2	28.4	21.0	14	20	3.29	32.3
17	3	3	29.7	21.0	.	20	3.42	35.4
18	3	1	39.8	29.0	22	25	2.96	51.4
18	3	2	36.2	26.0	20	22	3.46	49.8
18	3	3	33.5	27.0	.	20	3.04	38.6

ENT	YR	REP	CHL	HGT	TILLER	KERNEL	KERNEL WGT	YLD
19	3	1	37.8	26.5	35	17	3.32	75.1
19	3	2	38.9	26.0	32	16	3.44	87.1
19	3	3	42.2	26.5	.	19	3.36	107.8
20	3	1	38.6	23.0	17	26	2.86	47.6
20	3	2	38.7	21.0	14	27	2.66	35.7
20	3	3	33.9	23.0	.	27	2.92	47.5
21	3	1	36.4	23.0	29	25	3.42	91.9
21	3	2	32.0	21.0	22	23	3.24	61.6
21	3	3	35.4	22.0	.	23	3.24	68.1
22	3	1	41.8	22.5	24	22	3.44	76.7
22	3	2	38.6	21.5	23	23	3.38	72.6
22	3	3	38.2	23.0	.	23	3.34	70.1
23	3	1	34.1	20.0	25	20	3.20	61.4
23	3	2	33.0	21.5	25	22	3.46	62.4
23	3	3	32.0	20.0	.	21	3.28	60.1
24	3	1	31.4	24.0	28	37	3.54	88.9
24	3	2	34.7	27.0	29	32	3.70	81.1
24	3	3	34.0	25.5	.	34	3.52	93.7
25	3	1	34.3	18.0	28	17	3.38	67.1
25	3	2	35.6	22.0	30	19	3.79	71.1
25	3	3	33.1	22.0	.	17	3.45	61.0
26	3	1	33.1	21.0	16	20	3.06	64.1
26	3	2	30.4	21.0	18	19	2.96	56.0
26	3	3	.	.	.	.	.	.
27	3	1	30.3	19.5	19	20	3.42	68.3
27	3	2	31.0	22.5	17	21	3.54	69.8
27	3	3	31.6	22.5	.	20	3.38	78.1
28	3	1	28.4	20.0	11	15	3.05	31.2
28	3	2	26.5	19.0	12	16	3.34	27.8
28	3	3	26.1	22.5	.	18	2.98	28.5
29	3	1	.	.	.	.	.	.
29	3	2	.	.	.	.	.	.
29	3	3	.	.	.	.	.	.
30	3	1	33.7	25.0	29	22	2.66	61.5
30	3	2	34.3	25.5	28	20	2.71	67.5
30	3	3	38.6	28.0	.	27	2.61	78.3
31	3	1	36.9	19.0	20	33	3.41	40.3
31	3	2	36.8	21.0	25	29	3.74	44.2
31	3	3	39.5	22.0	.	28	3.34	48.5
32	3	1	33.2	22.0	.	.	.	.
32	3	2	35.1	22.0	31	23	2.99	78.8
32	3	3	41.8	23.0	28	23	3.29	82.2
33	3	1	38.5	26.0	28	27	3.94	114.0
33	3	2	37.7	28.5	29	33	3.72	106.3
33	3	3	36.1	26.5	.	33	3.61	97.9
34	3	1	34.8	21.0	34	27	3.11	67.6

ENT	YR	REP	CHL	HGT	TILLER	KERNEL	KERNEL WGT	YLD
34	3	2	34.2	22.0	30	26	3.15	70.4
34	3	3	32.4	24.0	.	27	3.31	74.1
35	3	1	35.0	25.0	25	23	2.74	44.2
35	3	2	31.0	23.0	30	26	2.61	42.6
35	3	3	35.5	23.5	.	30	2.83	47.7
36	3	1	30.2	23.0	19	19	3.01	62.1
36	3	2	27.4	23.5	18	18	3.22	56.0
36	3	3	31.9	24.0	.	18	3.14	59.6
37	3	1	34.2	24.0	29	27	3.90	77.1
37	3	2	35.0	22.0	20	27	3.18	51.1
37	3	3	33.6	21.0	.	25	3.35	60.7
38	3	1	34.6	27.0	17	24	2.66	78.1
38	3	2	34.2	23.0	15	14	2.66	54.1
38	3	3	29.0	23.0	.	23	2.85	63.5
39	3	1	32.5	19.0	22	22	3.01	43.2
39	3	2	35.8	21.0	24	20	2.98	54.7
39	3	3	31.0	21.0	.	21	3.24	53.0
40	3	1	30.3	24.0	23	25	2.78	47.4
40	3	2	30.8	24.0	20	23	2.81	50.3
40	3	3	28.2	25.0	.	22	3.21	53.6
41	3	1	31.9	18.5	26	27	3.15	51.7
41	3	2	30.3	19.0	25	24	2.96	52.3
41	3	3	31.4	20.0	.	23	2.92	49.0
42	3	1	37.7	23.0	28	21	3.22	83.0
42	3	2	36.2	22.0	25	23	3.04	84.3
42	3	3	37.4	25.5	.	22	3.94	91.1
43	3	1	.	.	.	.	.	.
43	3	2	.	.	.	.	.	.
43	3	3	.	.	.	.	.	.
44	3	1	35.8	23.0	25	23	3.28	74.3
44	3	2	37.4	24.0	25	23	3.51	81.0
44	3	3	37.2	24.0	.	25	3.44	81.8
45	3	1	32.7	23.0	23	29	2.62	56.2
45	3	2	32.9	21.5	20	17	3.41	46.6
45	3	3	24.0	19.0	.	17	2.16	39.6
46	3	1	36.4	22.5	25	21	3.02	60.8
46	3	2	36.7	24.0	21	20	3.34	52.5
46	3	3	34.1	24.0	.	22	3.21	67.8
47	3	1	44.4	28.0	28	30	3.84	131.5
47	3	2	41.4	28.0	26	28	3.78	122.4
47	3	3	40.5	29.5	.	33	3.80	125.6
48	3	1	38.7	27.0	28	19	3.36	59.1
48	3	2	38.1	24.5	25	17	3.41	61.0

ENT	YR	REP	CHL	HGT	TILLER	KERNEL	KERNEL WGT	YLD
48	3	3	36.0	25.0	.	20	3.46	56.3
49	3	1	32.3	24.0	24	21	3.64	34.1
49	3	2	30.7	24.5	24	19	3.56	39.8
49	3	3	30.3	25.0	.	20	3.24	32.2
50	3	1	37.7	21.5	23	21	3.19	38.3
50	3	2	39.1	21.0	23	19	2.88	44.8
50	3	3	38.1	19.0	.	20	2.84	32.1
51	3	1	33.0	22.0	22	18	3.45	52.8
51	3	2	32.5	21.0	24	19	3.64	64.4
51	3	3	33.8	23.5	.	21	3.51	63.8
52	3	1	38.7	20.0	28	23	3.24	87.6
52	3	2	41.9	24.0	38	23	3.07	81.5
52	3	3	38.8	21.0	.	21	3.44	106.5
53	3	1	28.0	21.0	16	16	3.15	35.8
53	3	2	33.6	25.0	19	19	3.44	58.8
53	3	3	36.2	27.0	.	29	3.68	72.6
54	3	1	33.4	26.0	20	21	3.21	60.9
54	3	2	34.2	25.0	18	22	3.04	55.3
54	3	3	36.3	24.0	.	29	3.08	50.2
55	3	1	37.2	24.0	25	21	3.20	49.5
55	3	2	38.5	24.0	24	23	3.42	56.0
55	3	3	.	.	.	.	.	.
56	3	1	36.6	28.5	26	15	3.28	49.6
56	3	2	36.4	25.0	29	17	3.49	40.6
56	3	3	35.0	28.5	.	33	3.42	72.9
57	3	1	27.7	22.0	25	22	3.52	53.4
57	3	2	28.3	24.0	24	27	3.24	59.4
57	3	3	33.5	26.0	.	23	3.42	64.9
58	3	1	32.2	24.0	29	20	3.36	94.0
58	3	2	32.0	22.0	30	21	3.26	88.3
58	3	3	32.1	23.0	.	18	3.18	78.5
59	3	1	34.2	21.0	24	20	3.54	69.7
59	3	2	34.9	22.5	26	18	3.34	59.3
59	3	3	35.5	22.0	.	19	3.24	54.5
60	3	1	30.7	26.0	24	25	3.04	44.6
60	3	2	30.6	29.0	24	25	3.04	41.0
60	3	3	30.1	26.0	.	29	3.01	45.0
61	3	1	28.5	23.0	14	24	3.25	52.4
61	3	2	30.5	23.0	13	22	3.18	55.3
61	3	3	34.1	25.0	.	24	3.61	60.1
62	3	1	38.1	27.5	22	28	4.40	79.8
62	3	2	38.7	26.0	19	28	4.14	73.0
62	3	3	38.8	28.0	.	30	4.25	72.5
63	3	1	32.1	22.0	25	19	3.45	74.3
63	3	2	30.5	22.0	24	17	3.36	61.2
63	3	3	32.8	24.0	.	22	3.62	85.0
64	3	1	.	.	.	.	.	.

ENT	YR	REP	CHL	HGT	TILLER	KERNEL	KERNEL WGT	YLD
64	3	2	33.5	25.0	29	19	3.71	85.7
64	3	3	30.1	23.0	.	20	3.52	70.0
65	3	1	36.1	20.0	22	28	3.34	91.7
65	3	2	37.3	20.0	20	26	3.14	86.8
65	3	3	35.9	.	.	.	.	.
66	3	1	32.0	25.0	22	31	3.35	70.0
66	3	2	35.4	26.0	26	33	3.46	76.1
66	3	3	.	.	.	.	.	.
67	3	1	33.7	25.0	28	27	2.91	71.0
67	3	2	31.8	24.0	27	24	3.02	76.4
67	3	3	33.1	25.0	.	21	3.14	73.1
68	3	1	36.3	22.0	20	26	3.22	68.3
68	3	2	33.9	21.0	20	24	3.31	63.7
68	3	3	32.8	21.0	.	24	3.12	61.8
69	3	1	39.7	22.5	25	25	3.34	77.2
69	3	2	33.1	22.0	22	25	3.45	80.3
69	3	3	33.7	22.5	.	27	3.62	81.1
70	3	1	32.4	23.0	17	24	3.41	64.7
70	3	2	34.6	24.0	19	23	3.34	63.0
70	3	3	32.9	24.0	.	29	3.47	64.0
71	3	1	33.2	25.0	26	26	3.10	68.5
71	3	2	31.4	25.0	24	28	3.30	77.5
71	3	3	36.3	27.0	.	32	3.64	82.9
72	3	1	28.1	21.0	17	26	2.89	45.0
72	3	2	31.6	22.0	30	24	3.28	64.6
72	3	3	29.1	23.0	.	29	3.08	39.6
73	3	1	28.7	19.0	22	15	2.64	28.9
73	3	2	29.9	19.0	24	17	2.76	22.2
73	3	3	31.4	22.0	.	18	2.68	31.5
74	3	1	29.8	23.5	22	29	3.55	52.9
74	3	2	26.1	23.5	24	28	3.46	44.5
74	3	3	27.0	24.0	.	28	3.48	41.1
75	3	1	30.0	23.0	16	27	2.74	39.8
75	3	2	31.2	23.0	15	24	2.68	37.3
75	3	3	30.0	23.0	.	26	2.82	41.0
76	3	1	38.6	20.0	28	36	3.06	73.2
76	3	2	37.2	20.0	25	32	2.87	66.6
76	3	3	38.6	18.0	.	39	2.98	63.5
77	3	1	39.2	31.0	29	41	3.55	92.6
77	3	2	39.5	30.0	28	42	3.51	93.2
77	3	3	37.8	30.0	.	38	3.42	80.8
79	3	1	40.7	29.0	19	34	3.51	93.7
79	3	2	40.0	25.0	19	30	3.68	100.5
79	3	3	42.2	30.0	.	33	3.43	129.3
80	3	1	31.4	26.0	17	38	3.28	61.7
80	3	2	38.7	24.0	19	37	3.61	68.5
80	3	3	34.1	26.0	.	38	3.55	79.3

VITA

Agron Collaku was born on August 9, 1958, in Permet, Albania. He graduated with a bachelor of science degree in agronomy from the Agricultural University of Tirana, in 1983, and was awarded a Golden Diploma for a 10.0 GPA (equivalent to 4.0 in the USA). In 1985, he was appointed as instructor of Agricultural Experimentation and Plant Breeding, at Agricultural University of Tirana. In 1988 he was awarded a fellowship from Food and Agricultural Organization, for training in quantitative genetics at University of Milan, Italy. He received a “Candidate of Sciences” degree (similar to a master of science degree in the USA) in Plant Breeding from the Agricultural University of Tirana, in 1991, and became an assistant professor. He taught agricultural experimentation, a basic course in statistics, and plant breeding, and published several papers on quantitative genetic research in international and Albanian journals.

He won a research Fulbright Scholarship from US Council of International Exchange of Scholars in 1995, and came to Louisiana State University, Department of Agronomy, as a visiting scientist. Here, he completed a quantitative genetic project on “Clustering of soft red winter wheat trials in southern region”. In 1996, he enrolled in the Graduate School of Louisiana State University, pursuing a doctoral degree in agronomy, and a master in applied statistics. His research is in the field of quantitative genetics with application in wheat breeding. He has presented papers in several meetings. He is a member of American Society of Agronomy, Crop Science Society of America and American Statistical Association. He is now a candidate for the Doctor of Philosophy degree in agronomy, in the field of quantitative genetics.

DOCTORAL EXAMINATION AND DISSERTATION REPORT

Candidate: Agron Collaku

Major Field: Agronomy

Title of Dissertation: Heritability of Waterlogging Tolerance in Wheat

Approved:

Major Professor and Chairman

Dean of the Graduate School

EXAMINING COMMITTEE:

Date of Examination:

25 September 2000