INHERITANCE OF NITROGEN USE EFFICIENCY COMPONENTS IN SOUTH AFRICAN IRRIGATED WHEAT

by

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DECLARATION

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

Signed on the --------- of ---------------- 2007 at the University of the Free State, Bloemfontein, Republic of South Africa.

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LIST OF ABBREVIATIONS

%	- Percentage
°C	- Degrees Celcius
Ca^{2+}	- Calcium
cm	- centimeter
Cu	- Copper
GCA	- General combining ability
H^2_b	- Broad-sense heritability
H^2_n	- Narrow-sense heritability
ha	- hectare
HI	- Harvest index
HN	- High nitrogen treatment
K	- Potassium
KCl	- Potassium chloride
kg/ha	- kilogram per hectare
LN	- Low nitrogen treatment
m^2	- square meter
Mg	- Magnesium
Mt	- Million tons
N	- Nitrogen
NAE	- Nitrogen agronomic efficiency
NH_3	- Ammonia
NH_4^+	- Ammonium ion
NHI	- Nitrogen harvest index
nm	- nanometer
NO_3^-	- Nitrate ion
NPE	- Nitrogen physiological efficiency
NRE	- Nitrogen recovery efficiency
NUE	- Nitrogen use efficiency
NupE%	- Nitrogen uptake efficiency percentage
NutEYld	- Nitrogen utilization efficiency for grain yield
P	- Phosphorus
SAGIS	- South African Grain Information Service
SCA	- Specific combining ability
t/ha	- ton per hectare

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CHAPTER 1

INTRODUCTION

Wheat is one of the important grain crops produced worldwide. It is cultivated on all the continents of the world, easily stored and transported, and an important nutritional source for humans. World production of wheat in 2002 amounted to 572.879 million tons (Mt), and together with rice (576.280 Mt) and maize (602.589 Mt), these are considered the most important grain crops. In South Africa, between 1.27 Mt (1992/93) and 3.49 Mt (1988/89) of wheat is produced annually with a total domestic consumption of 2.781 Mt for the 2005/2006 period (SAGIS, 2007). Demand is determined mainly by the need for the end products, *viz*. bread, other processed products and private consumption of flour (FAO, 2002).

Wheat is cultivated in various regions of South Africa, with up to 36% of the total annual wheat harvest produced in the summer rainfall area under irrigated conditions (Wheat Board, 1996; Fletcher, 2004). It is estimated that 1498000 ha was planted to arable crops, with 941000 ha planted to wheat in 2002 (FAO, 2002). The National Crop Estimates Committee listed the proposed area of irrigated wheat to be planted in 2006/2007 at 22% of total hectares planted to wheat (SAGIS, 2007).

Yield levels and quality of produced grain play an important part in the successful and economic production and marketing of wheat. Traditionally, yield was economically the most important factor to the producer. However, as the end user became more demanding with regards to quality of the end product, linked to the possibility of exporting surplus production combined with higher quality standards required, the quality of produced grain became more important. The current grading system for wheat in South Africa includes hectolitre mass and grain protein percentage as part of the quality parameters to determine the marketability of wheat. Protein quantity and quality directly affect the flour protein and dough characteristics. Therefore, low protein grain is penalised by a lower price per ton, leading to significant economic losses for the wheat producer.

Low soil nitrogen (N) availability is often the major nutrient factor limiting the yield of crop plants (Andrews *et al*., 2004). As the effect of additional N on crop yield is usually substantial and cost-effective, the strategic application of inorganic N fertilizer has become an important tool used to increase crop yields in intensive agricultural systems

(Andrews *et al*., 2004). Optimum N management for wheat production is thus important for economic yield, optimum water utilization and minimum pollution of the environment (Corbeels *et al*., 1999). Excluding available soil water, N is the next most limiting factor in local wheat production as in other wheat production areas worldwide (Nielson & Halvorson, 1991; Campbell *et al*., 1993). Nitrogen frequently limits grain yields and grain protein percentage, and additional N inputs are required to optimise productivity and profitability.

Nitrogen is currently the most widely used fertilizer nutrient and the demand for it is likely to grow in the near future (Godwin & Jones, 1991). Loss of fertilizer results from surface runoff, leaching, soil denitrification, volatilisation and gaseous plant emission. Also, N fertilizer is one of the most expensive inputs used in present day wheat production (Ehdaie *et al*., 2001). Because of this, there is a need to reduce the use of N fertilizer and search for plant genotypes with greater N use efficiencies, either in a strict physiological sense (increased carbon (C) gain per unit N), or in an agronomic sense (increased dry matter or protein yield per unit plant N or per unit N applied/available to the crop) (Andrews *et al*., 2004). Thus, the efficiency of wheat cultivars in N use has become increasingly important, as greater N use efficiency could allow a reduction in N fertilizer use without a decrease in yield.

Total fertilizer use in South Africa (2002) was 482000 ton of N, 101000 ton of P, and 135000 ton of K fertilizer products (Humphris, 2003). The domestic consumption of fertilizers was the highest since 1983, with the 1990 - 1999 average use of N, P and K at 386000, 103000 and 111000 tons respectively.

The major small grain cereal growing areas of South Africa and especially the Summer Rainfall Region have in recent years experienced declining crop yields and grain protein contents, especially in a wheat monoculture cropping system. With changes in the marketing system of wheat in South Africa, the quality of produced grain, especially with regards to grain protein content, has become increasingly important. Profitability of wheat production thus depends on yield and grain protein content, with available N influencing both (Dalal *et al*., 1998).

Increased N fertility can stimulate deeper rooting of wheat, making a greater quantity of stored soil water available to the plant, thereby reducing potential water stress. However, larger aboveground biomass stimulated by increased N availability results in greater transpiration demands (Ritchie & Johnson, 1990). Thus, if sufficient water reserves were not available, greater water stress in high N environments would occur, possibly during the later critical crop development stages, thereby reducing the yield. Continuous cereal cropping without N inputs from fertilizers or legumes has led to widespread deficiency of N in wheat (Doyle & Holford, 1993). This has occurred on soils previously regarded as high in available N and which have produced high grain protein wheat for relatively short periods (< 40 years) of wheat production.

The utilisation of N by higher plants involves several processes including, uptake mechanisms, storage, translocation, reduction and incorporation into organic forms (Moll *et al*., 1982). Under conditions of limited supply of N, remobilization of previously assimilated N can occur by breakdown of insoluble protein sources. Under these conditions, most of the N in wheat grain can be derived from remobilization, whereas under conditions where N absorption is possible during grain development, remobilization may be less than 50% of grain N. Plant uptake of N and N concentration of plant material is linked to the specific plant developmental stage, N supply and subsequent redistribution of N within the different plant parts. Nitrogen requirement is therefore related to total N removed by the crop (Osaki *et al*., 1991). Plant analysis can provide an effective means of monitoring the nutritional status of a crop. If critical tissue concentrations are known, potential deficiencies can be identified before visual symptoms appear, and additional nutrients applied before yields are reduced (Vaughn *et al*., 1990).

The probable response to applied N fertilizer is therefore dependant on the size of available and potentially available pools of N in the soil, and the N demand of the crop as determined by dry matter production and minimum tissue N concentration. Measurement of the soil mineral N content at planting can be a useful aid in determining optimum fertilizer levels, and an indication of the potential available N through mineralization of soil organic matter can further improve N recommendations. The available soil water and tillage methods also affect the quantity of residual soil mineral N available. The measurement of residual N in the soil profile should include critical variables like depth, time of sampling, and number of samples to account for spatial variability. The many transformation pathways and multitude of factors affecting the dynamics of N in soils, renders it a complex plant nutrient to study. Nitrogen recommendations must incorporate the various factors influencing N in the soil-plant system, which will enable situation-specific recommendations.

Variations in climate and cultural conditions influencing plant growth, mineralization and

N uptake can result in varying N availability indices from year to year, making the accurate prediction of fertilizer N requirement difficult. To overcome this problem, direct and indirect measurements of soil and plant mineral N and plant response to N fertilizer have been used. For soils, these include measurement of soil mineral N content, organic matter and N mineralization, as well as measuring and predicting potentially available N and losses from the soil. For plants it includes total plant uptake and N concentration, and the use of physiologically based crop models. The N requirement of a wheat cultivar is influenced by yield, N content and efficiency of N uptake from the soil, and the availability of N fertilizer to supplement soil N supply as influenced by immobilization, leaching and gaseous losses (Broadbent, 1981; Rice *et al*., 1995).

The traditional objectives of the wheat breeder are to develop cultivars with a stable and high yield and good grain quality characteristics. For the effective improvement of quality and yields, a plant breeder must have knowledge of the inheritance of quality traits and the joint inheritance of quality and agronomic characteristics (Baker *et al*., 1971). There is limited information available on the N use efficiency components of wheat cultivars currently cultivated under irrigation. The use of more N efficient cultivars can either reduce N applications or reduce the environmental risk related to high N use in agriculture. The efficient use of N in the soil-plant system can also result in cultivars producing high yields with high grain protein.

It is therefore evident that N is an important plant nutrient, and that studies aimed at improving N fertilizer use efficiency and crop response should include the following objectives:

- Assess the yield, N uptake and N use efficiency of selected irrigated wheat cultivars by comparing the different agronomic and physiological N use efficiency components.
- Determine the general and specific combining abilities of irrigated cultivars for the N use efficiency components.
- Determine the correlations between different characteristics and efficiency components.
- Determine the broad and narrow sense heritability for the measured and calculated characteristics and components.

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CHAPTER 2

GENERAL LITERATURE REVIEW

2.1 Extent of wheat production

Wheat (*Triticum aestivum L.*) is one of the world's most important grain crops. It is cultivated on all the continents of the world, easily stored and transported, and an important nutritional source for humans (Slafer & Satorre, 1999). World production of wheat in 2002 amounted to 572.879 million tons (Mt), and together with rice (576.280 Mt) and maize (602.589 Mt), these grain crops are the most important grain crops. In South Africa, between 1.27 Mt (1992/93) and 3.49 Mt (1988/89) of wheat is produced annually with an estimated total domestic consumption of 2.781 Mt for the 2005/2006 period (SAGIS, 2007). Total domestic wheat demand was estimated for the 2004/2005 season at 2.879 Mt (Fletcher, 2004). Demand is determined mainly by the need for bread, other processed products and private consumption of flour (FAO, 2002). It is estimated that 1498000 ha was planted to irrigated crops, with 941000 ha planted to wheat in 2002 (FAO, 2002). The National Crop Estimates Committee listed the proposed area in South Africa to be planted to irrigated wheat in 2006/2007 at around 22% of the total of 885500 ha (SAGIS, 2007).

Yield levels and quality of produced grain play an important part in the successful production and marketing of wheat, and efficient N inputs must be economically feasible and environment friendly. Traditionally, yield was economically the most important factor to the producer. However, as the end user became more demanding concerning product quality, linked to the possibility of exporting surplus production combined with higher quality standards required by industry, the quality of produced grain became more important. The current grading system for wheat in South Africa includes hectolitre mass, grain protein percentage and falling number as part of the quality parameters to determine the marketability of wheat. Protein quantity and quality directly affect the flour protein and dough characteristics. Therefore, low quality grain is penalised by a lower price per ton, leading to significant economic losses for the wheat producer.

2.2 Importance of N in wheat

Nitrogen (N) is currently the most widely used fertilizer nutrient and the demand for it is likely to grow in the near future (Godwin & Jones, 1991). Domestic consumption of fertilizers is currently the highest since 1983. Total fertilizer use in South Africa (2002) was 482000 ton of N, 101000 ton of phosphorus (P) and 135000 ton of potassium (K) fertilizer products (Humphris, 2003). The average use of fertilizers for the 1990 -1999 period was 386000 on for N, 103000 ton for P, and 111000 ton for K products respectively.

Nitrogen is a major essential nutrient required by plants in substantial quantities. The many transformation pathways and multitude of factors affecting the dynamics of N in soils, renders it a complex plant nutrient to study. Excluding available soil water, N is the next most limiting factor in wheat production as in other worldwide wheat production areas (Nielson & Halvorson, 1991; Campbell *et al.*, 1993). Nitrogen frequently limits grain yields and grain protein concentration, and additional N inputs are required to optimise productivity and profitability. Nitrogen has been one of the most investigated factors over time in wheat production. Numerous studies indicated that N fertilization can increase both wheat grain yield and grain protein concentration, but that a lag period in N response exists between grain yield and grain protein concentration. Grain yields are preferentially increased up to a maximum biological level, with grain protein remaining at a constant value. Only thereafter grain protein increases with additional N applications. Grain protein thus responds to higher levels of N application than does grain yield (Ma *et al*., 2004).

The aim of a producer is to increase yields with a consequent economic return from the additional fertilizer costs. Traditionally yield information from field experiments that tested increasing levels of a nutrient was used to calculate response curves to indicate how yield was influenced by the nutrient application. These response curves formed the basis for calculating optimum fertilization requirements. Accurate fertilizer N recommendations are therefore important for cost-effective and environmentally friendly agricultural production (Halvorson *et al*., 1987). Nevertheless, optimum N management for wheat production is important for maximum economic yield, optimum water utilization and minimum pollution of the environment (Corbeels *et al*., 1999).

2.3 Utilization of N by plants

Efficient use of fertilizer N is becoming increasingly important in crop production due to rising costs associated with fertilizer N production and growing concern about nitrate contamination of ground and surface waters.

2.3.1 Form, time and method of N application

Nitrogen should be available when required by the crop to maximize use. The most effective time for N application generally coincides with the period of rapid N uptake by the plant (e.g. grain formation and filling) (Jenner *et al.*, 1990). Application at this time reduces the opportunity for N losses, and results in the applied N being available throughout the period of grain formation and growth (Olson & Kurtz, 1982).

2.3.2 Functions and movement of N in plants

A requirement for N exists throughout the development of a plant to maintain growth, as N is a constituent of both structural (e.g. cell walls) and non-structural (e.g. enzymes, chlorophyll, and nucleic acids) components of cells. Most N for vegetative growth is supplied either by the assimilation of (i) N absorbed from the soil and/or (ii) N fixed from atmospheric N_2 in the case of leguminous crop species (Schrader, 1984). Both the xylem and phloem participate in transporting N in plants (Pate, 1973).

The xylem is the principle path for long distance transport of nitrogenous solutes from the roots to organs that transpire (Pate, 1973; Schrader, 1984). The xylem therefore transports NO_3^- from the roots to shoots in addition to N reduced to NH_4^+ in the roots (Schrader, 1984). The phloem is the principal transport path of N assimilated in one part of the shoot and transported to another (e.g. leaf to seed). In contrast to the xylem, N solutes in the phloem are organic solutes, with nitrate usually absent or present only in trace amounts in the phloem (Pate, 1976).

2.3.3 Processes of N uptake

The utilization of N by higher plants involves several processes, including uptake, storage, translocation, reduction and incorporation of N into organic forms. The predominant form of N available to plants is NO_3^- because under most soil conditions NH_4^+ is rapidly nitrified to NO_3^-. Ammonium is however, the major form of N available to plants under conditions that are unfavourable for nitrification. Ammonium cannot accumulate in cells to any great extent without damage to the plant. Because of this, it is normally converted to amino acids or amides in the root and translocated to the tops in these organic forms (Haynes, 1986c). Nutrients destined for use by the plant must first move through root tissues before entering the xylem, and being translocated to the shoots. Absorption of ions across the plasmalemma of root cells is generally accepted to be an active process that often overcomes an unfavourable electrochemical gradient through the expenditure of energy (Haynes, 1986c; Marchner, 1995).

2.3.3.1 Ammonium uptake

The time dependant uptake of NH_4^+ by plants can be characterised by two phases. The initial phase (not inhibited by low temperatures or metabolic inhibitors) represents passive exchange-absorption process in the negatively charged free space of roots (Nye & Tinker, 1977). The second phase of uptake is sensitive to low temperatures and metabolic inhibitors and represents active absorption of NH_4^+ (Nissen *et al*., 1980).

2.3.3.2 Nitrate uptake

Uptake of NO_3^- by plants is an energy requiring process, and is restricted by inhibitors of RNA and protein synthesis, and inhibitors of respiratory and oxidative phosphorylation (Jackson *et al.*, 1973; Rao & Rains, 1976; Tompkins *et al*., 1978). It is generally thought that NO_3^- transport across the plasmalemma is linked to a membrane-bound ATPase (Huffaker & Rains, 1978).

2.3.3.3 Factors affecting uptake

Uptake rates of NH_4^+ are normally unaffected by the presence or absence of NO_3^- in the nutrient solution, but ambient NH_4^+ has been shown to restrict net NO_3^- uptake (Rao & Rains, 1976; Youngdahl *et al.*, 1982). This inhibitory effect of NH_4^+ on NO_3^- uptake is, in the majority of cases, independent of any such effect on NO_3^- reductase enzyme activity. Active uptake of anions across the plasmalemma of roots involves active excretion of OH^- or HCO_3^-, while uptake of cations results in excretion of H^+ (Nye, 1981). With NH_4^+ nutrition, the plant absorbs cations in excess of anions, so that plant growth results in the net efflux of H^+ ions into the rhizosphere, with a resultant decrease in the soil pH close to the root (Smiley, 1974). When NO_3^- is the major form of N supplied, plants absorb an excess of anions, and there is a net efflux of OH^- or HCO_3^- ions. Consequently, there is an increase in rhizosphere pH (Smiley, 1974).

Generally, NH_4^+, Ca^{2+}, Mg^{2+} and K^+ compete with each other during ion accumulation by plants, with NH_4^+ uptake reducing K^+ uptake (Haynes & Goh, 1978) and *vice versa*. Ammonium nutrition results in increased uptake of phosphate and sulphate, mainly because of the lowering of rhizosphere pH. Nitrate nutrition generally stimulates cation uptake and inhibits that of anions (Haynes & Goh, 1978). Because uptake of NO_3^- and NH_4^+ are active processes, carbohydrate (energy) supplies influence both processes, so that energy supply to the roots to sustain the uptake system is important. Low light intensities reduce uptake of both forms of N. Their uptake shows diurnal variation that is linked to translocation of photosynthates from the leaves and thus the availability of carbohydrate reserves in the roots. Nitrate uptake is restricted more by low temperatures than is the uptake of NH_4^+, while at around 23 to 35 °C, NO_3^- uptake exceeds that of NH_4^+ (Frota & Tucker, 1972).

2.3.4 Processes of assimilation

The first step in the assimilatory reduction of NO_3^- in higher plants is catalysed by the enzyme complex nitrate reductase. The enzyme catalyses the reduction of NO_3^- to NO_2^- by reduced pyridine nucleotides (Guerrero *et al.*, 1981), as follows;

$$NO_3^- + NAD(P)H + H+ \overset{2e-}{\Leftrightarrow} NO_2^- + NAD(P) + H_2O$$

The next step is the reduction of NO_2^- to ammonium in photosynthetic cells and is catalysed by the enzyme ferrodoxin-nitrite reductase.

$$NO_2^- + GFd_{red} + 8H^+ \overset{6e-}{\Leftrightarrow} NH_4^+ + GFd_{ox} + 2H_2O$$

Ammonia assimilation has a central role in plant N metabolism, since NH_4^+ is absorbed directly by the roots, and it is the product of NO_3^- and urea assimilation, and molecular nitrogen fixation (Miflin & Lea, 1980). The major pathway of ammonia assimilation is through the glutamate synthase cycle, catalysed by the enzymes glutamine synthetase and glutamate synthase (Miflin & Lea, 1980). The initial incorporation of NH_3 into the amide position of glutamine is catalyzed by the enzyme glutamine synthetase (Haynes, 1986c). In the presence of a reducing source, glutamate synthase catalyzes the transfer of the amide group of glutamine to α-oxoglutarate resulting in the formation of the amino acid glutamate. The incorporation of the NH_4^+ into an amino acid is then followed by transamination reactions in which the amino group is transferred to another metabolite thus forming other amino acids or amino compounds (Haynes, 1986c). The NH_4^+ is incorporated into amino acids that are then assembled in specific sequences to form different proteins (Larsen, 1980).

Ammonium is extremely toxic if it accumulates in plant tissues, and plants generally lack any mechanism to deal with its accumulation other than assimilation. The control of N metabolism however tends to ensure that NH_4^+ is not generated internally under conditions such that it cannot be assimilated (Guerrero *et al.*, 1981). Givan (1979) has suggested that at high levels of tissue NH_4^+, the enzyme asparagine synthetase could also become a primary assimilating enzyme.

2.3.5 Foliar applications

Urea is widely used in foliar application of N, and it can penetrate rapidly through the cuticle into leaf cells. Foliar applied urea is metabolised in the plant to NH_3 and CO_2 by the enzyme urease (Rachpahl-Singh & Dirk, 1993). Plant foliage can also absorb NO_2 and NH_3 gases from the air (Farquhar *et al.*, 1983; Marchner, 1995). This is assumed to be by diffusion into stomata and then into the intercellular spaces of leaves (Kannan, 1980).

2.3.6 Reponses to limiting or oversupply of N

In natural ecosystems, the rate of N mineralization shows a distinct seasonal trend with peaks in availability, resulting in high concentrations of mineral N, followed by periods of low supply (Taylor *et al.*, 1982). Plants take advantage of these transient levels of mineral N and show similar seasonal patterns of N uptake and in the activity of N assimilating enzymes (Taylor *et al.*, 1982). However, in agricultural ecosystems, fertilizers are commonly added to facilitate maximum growth, and these applications can result in an oversupply of mineral N. Toxic reactions can occur when NH_4^+ accumulates in plants, but in contrast, plants can accumulate high concentrations of NO_3^- and transport it through the plant with few toxic effects (Mills & Jones, 1979). Phytotoxic effects of NH_4^+ usually do not occur in fertile soils because of rapid nitrification, but heavy applications of ammoniacal fertilizers to cool and wet soils can result in the accumulation of toxic levels of NH_4^+ (Haynes, 1986c; Marchner, 1995). Although plants can accumulate high concentrations of NO_3^-, health problems can result when humans or domesticated animals ingest such plant material (Mills & Jones, 1979). Both NH_4^+ and NO_3^- oversupply results in the depletion of the plant's supply of storage carbohydrates that are used during assimilation of NH_4^+ (Michael *et al.*, 1970). Although Mengel & Kirkby (1979) reported a decrease in wheat yields at high N fertilization in their studies, van Rensburg (1996) did not measure a significant reduction in grain yields in a study with a South African irrigated wheat cultivar.

2.3.7 Factors affecting crop response to N

Nitrogen management is the key to establishing a balance between yield and quality of the grain produced and systems of N management must be directed towards these specific objectives. The major small grain cereal growing areas of South Africa and especially the Summer Rainfall Region have in recent years experienced varying crop yields with variable grain protein concentration. With changes in the marketing system of wheat in South Africa, profitability of wheat production now depends on yield and grain protein content, with N availability influencing both (Dalal *et al.*, 1998).

Economic responses of crops to fertilizer N additions occur as increased yield or protein yield, or quality improvement. The simplest response of plants to applied N, when N is the limiting factor, is a linear increase in dry matter production with rates up to the maximum application rate of N, staying constant thereafter or declining (Bock, 1984). The application of N to cereals commonly results in increasing biological yield (Donald & Hamblin, 1976), also with significant effects on dry matter production through the stimulation of vegetative growth and ultimately grain yields (du Plessis & Agenbag, 1994). The magnitude of response to applied N is dependant on the size of the available and potentially available pool of N in the soil, and the demand by the crop as determined by its potential biomass production and related minimum tissue N concentration (Olson & Kurtz, 1982). The response of crops to N is modified and affected by environmental factors from season to season (Keeney, 1982).

Insufficient N availability for maximum crop production is characteristic of soils all over the world. The problem is often acute in regions where soils typically have low organic matter contents. Engel *et al*. (2006) confirmed this response reporting that the instances of N deficiency in the Northern Great Plains have increased over time due to a lack of indigenous soil N. Any system designed to increase crop production must therefore include additional inputs of N and improved efficiency of N utilization (Broadbent, 1981). Optimal utilization of N in annual crop production requires a balance between the supply of N, from both fertilizer and mineralization of soil organic matter, and crop demand. However, in most cropping environments, availability of N may be out of phase with crop demand (Angus & Moncur, 1985). High efficiency of fertilizer N use by crops should be expected when N availability matches crop needs throughout the growing season. Understanding the N uptake pattern of wheat linked to N availability is therefore important for improving N fertilizer management (Baethgen & Alley, 1989a). Optimum N rates are difficult to predict for a particular site and year because of variability in soil moisture content and temperature, which greatly affect microbial N transformations (Franzluebers *et al*., 1995). Response to N fertilizer is strongly dependant on supply of non-fertilizer N in a given year, and the yield of unfertilised plots was not related to the maximum yield of fertilized plots over time (Johnson & Raun, 2003).

A major obstacle in the development of reliable methods for predicting crop N requirements is the difficulty in identifying and quantifying factors that consistently affect N responses, and the variability that occurs between growing seasons (Goh & Haynes, 1986). Several factors have been identified that affect the response of wheat to N (Keeney, 1982). Tiller production can be important in determining eventual grain yield, and is closely associated with rate of leaf emergence (Simmons, 1987). Cessation of tillering is associated with the completion of spikelet initiation on the main shoot and the beginning of stem elongation (Simmons, 1987). Reducing early tiller senescence might be achieved through plant breeding or N management, and preventing pre-anthesis water stress (Simmons, 1987).

The double ridge stage on the shoot apex has traditionally been regarded as the beginning of spike development (spikelet initiation). Initiation of the terminal spikelet marks the end of spikelet formation. The control of N movement into the kernels may be independent of carbohydrate movement, implying that the cause of low N concentration into the grain is inadequate supply of N to the kernels (Simmons, 1987). Nitrogen uptake by a kernel is linear over much of the grain filling period, and N can accumulate under optimal conditions at a rate of 0.03-0.04 mg kernel^{-1} day^{-1}. Leaf area index of a wheat crop reaches its peak before anthesis and then declines as leaf senescence progresses towards maturity.

Grain yield may be positively related to the duration of leaf area, and environmental conditions such as soil water or N stress can hasten senescence and reduce leaf area duration (Simmons, 1987). Nutrient uptake depends on both the inherent physiology of the plant and the availability of nutrients to the roots. Under field conditions without later additional N applications, N uptake is usually low following heading. However, under favourable post anthesis conditions a large proportion of the final grain N can be derived from N taken up during grain filling (Simmons, 1987). In general, high levels of N result in higher grain protein in wheat and increased efficiency of N utilization is realized when the N concentration in the kernels increases and the grain yield remains stable (Kramer, 1979).

2.3.7.1 Available soil water

A positive interaction between fertilizer N and applied irrigation or available soil water often occurs (Goh & Haynes, 1986; Bonfil *et al.*, 1999). When plant growth and yields are limited by available water, the N requirement is relatively low, but with sufficient water available, crop growth is greatly increased and therefore also N requirement (Goh & Haynes, 1986). Engel *et al*. (2006) observed that excess N applications lead to yield reductions under soil water limited environments as in summers of high temperatures.

2.3.7.2 Cultivation and residue management

Primarily cultivation disturbs the soil, increases soil porosity and aeration, exposes less accessible organic substrates to biological mineralization and results in a flush of mineralization of organic N (Wong & Northcliff, 1995). The incorporation of large amounts of residues (with high C:N ratios) can result in immobilization of mineral N in the cultivation zone and thus a reduced release of N over time for crop use. Losses of N from irrigated systems can include increased leaching losses and greater denitrification losses of N_2O and N_2 due to a higher water content and a source of readily available C in the cultivation zone of the soil (Rice & Smith, 1982).

Crop residue management alters many soil properties; physical, chemical, biological and thereby nutrient transportation and efficiency of use (Power & Doran, 1988). Residue management during the fallow period will also affect potential soil mineral N availability, and hence probable response to applied N fertilizer. Incorporation of crop residues with high C:N ratios immobilize soil and fertilizer N, and can reduce yields where initial soil mineral N levels are low by reducing N availability and thereby depressing early crop growth (Robson & Taylor, 1987; Power & Doran, 1988). Generally, in high yielding double-cropping environments under irrigation, the amount of residue added in combination with conventional cultivation practices, lead to significant amounts of crop residues remaining in the cultivation zone at planting because of the limited time available for decomposition. This undecomposed residue in the cultivation soil layer at planting affects the availability of soil mineral N to the growing crop mainly because of soil mineral N immobilization during continued decomposition of these residues.

Organic materials with low N concentrations and/or wide C:N ratios such as wheat residue will generally result in net immobilization of soil mineral N for a longer period of time, than materials having a high N concentration and a narrower C:N ratio (Robson & Taylor, 1987; Power & Doran, 1988). Organic materials with C:N ratios of 25 or less, and N concentrations of above 1.5% are required for net mineralization to occur quickly (Campbell, 1978; Haynes, 1986b). Efficient synchronization of mineralization and N availability with crop N demand is linked to N management (Parr & Papendick, 1978). Harper & Lynch (1981) and Mason & Rowland (1992) found that fewer tillers and lower yields were produced when wheat was planted in undecomposed crop residues and attributed this response mainly to the immobilization of soil mineral N by microbial decomposers, resulting in low soil mineral N availability to the growing crop.

2.3.8 Assessment of N availability

Between 97 and 99% of the N in soils is present in organic forms that are not directly available to plants until after mineralization has occurred. The amount of N mineralized depends on temperature, water and other environmental factors and is therefore difficult to predict (Goh & Haynes, 1986). Because N is taken up from the soil, plant available soil mineral N has a direct influence on grain protein and yields (Smika & Greb, 1973; Fowler *et al.*, 1990). Porter *et al.* (1982) linked soil factors important in determining grain protein to the depth of mineral N in the soil profile. This is because nutrients deep in the soil profile are only exploited late in the plant's development.

Soil measurements of N are taken at the beginning of the growing season, whereas yield responses to N fertilizer will be modified by seasonal weather and soil conditions (McDonald, 1989). Soil mineral N content is reduced by crop growth during the winter, but in spring mineralization rates can increase and possibly make a significant contribution to the N requirement of the wheat crop (McGarity & Myers, 1973). Consequently, the ability of soil tests of mineral N to account for differences in grain yield between sites and seasons are often low (Taylor *et al.*, 1988; McDonald, 1989).

Critical variables in estimating residual mineral N in the profile include; depth of sampling, time of sampling, and number of samples taken from a field (Goh & Haynes, 1986). The effective rooting depth of a crop determines the depth of sampling required to adequately assess the quantities of residual N available in the soil profile. Factors such as soil type, presence of impeding soil layers and distribution of nutrients and water in the soil profile can influence rooting depth. Sampling must be done shortly before planting of the crop, or early in the growing season so that the pool of mineral N available to the crop can be adequately estimated (Halvorson *et al.*, 1987).

The use of soil mineral N content in humid regions has been reported to be too variable to be a good indicator of N availability to crops (Fox & Piekielek, 1978). Several efforts have been made to develop suitable soil testing procedures aiding optimum N fertilizer rate prediction. Residual soil mineral N and/or mineralisable organic N indices have been used in areas where leaching of NO_3^- from the root zone is minimal (Baethgen & Alley, 1989b). Hadas *et al.* (1989) evaluated soil N mineralization (up to 120 cm in the profile) *in situ* in plots with and without N fertilizer. These authors also suggested that a potentially successful approach for assessing wheat N requirement should include plant tissue testing for N concentration during different stages of crop growth.

Rice *et al.* (1995) stated that the plant is the ultimate integrator of all the environmental variables controlling the N transformations within the soil cycle. Nitrogen uptake by an unfertilized crop is considered by many to represent the best method for quantifying net N mineralization (Broadbent, 1981). The advantage of this approach is that it integrates field temperature, water and aeration conditions that influence N mineralization potential.

There are two major types of soil tests for N (Goh & Haynes, 1986; Campbell *et al.*, 1995);

- residual mineral N in soil profile is measured and fertilizer recommendations are modified depending on the amount present;
- the complementary approach is to obtain an estimate of the amount of potentially mineralisable N present in the soil.

The above tests are based experimentally on incubation methods and chemical extraction methods, collectively known as N availability indices.

Inorganic nitrogen (NO_3^- and NH_4^+) in the soil was extracted with 1N KCl (10 g soil:100 ml KCl) during a 30 minute end over end shaking, and after filtration analyzed by the colorimetric flow system method (Keeney & Nelson, 1982; Technicon, 1977, 1978). The basic analytical steps for NO_3^- are: NO_3^- reduction to NO_2 with a modified *Griess-Millosvay* procedure by diazotizing with sulfanilamide and coupling with N-(1-naphtyl)-ethylene-diamine to form a purple-colored dye, which is measured by absorbance at 520 nm (Keeney & Nelson, 1982), following the automated Cu-Cd reduction technique using a Technicon autoanalyzer system (Technicon, 1977; 1978).

Soil NH_4^+ was determined by reacting NH_4^+ with phenol and hypochlorite in an alkaline solution to form an intense blue color that is measured by absorbance at 630 nm. This colorimetric procedure is widely known as the *Bethelot* reaction or the indophenol blue method (Keeney & Nelson, 1982). It is usual practice to extract exchangeable NH_4^+ and NO_3^- from field-moist soil samples. The decision to use air-dried samples in this study was motivated by the practical difficulty of using field-moist samples for routine analysis (Wiltshire & du Preez, 1994), and the potential for delays in transporting samples from distant localities to the analytical laboratory at Bethlehem. It is accepted that small changes in mineral N content of samples may have occurred during air-drying. The most frequently observed changes are a small increase in exchangeable NH_4^+ and some loss of NO_3^- although no significant changes are usually observed (Sereviratne & Wild, 1985; Wiltshire & du Preez, 1994).

2.3.8.1 Potentially available N

Nitrogen availability indices are a measure of the potential of a soil to supply N to plants. Since mineralization is affected by many environmental and cultural factors, such indices can only give an indication of the amount of N that will be potentially mineralized under field conditions (Haynes, 1986b). The indices can be divided into biological (aerobic and anaerobic incubations) and chemical methods (Bundy & Meisinger, 1994; Hart *et al.*, 1994).

Measurement of the soil mineral N content at planting can be a useful aid in determining optimum fertilizer levels, and an indication of the potential available N through mineralization of soil organic matter can further improve N recommendations. The available soil water and tillage methods also affect the quantity of residual soil mineral N available. The measurement of residual N in the soil profile should include critical variables like depth, time of sampling, and number of samples to account for spatial variability. Soil analysis is a first guide to efficient fertilization. Nitrogen is mobile in the soil and is subject to leaching and denitrification losses. Soil testing for N requires soil samples to a depth of at least 60 cm to estimate the level of plant available N. Sampling to 120 cm is recommended to improve the accuracy of N recommendations (Halvorson *et al.*, 1987).

2.3.8.2 Residual soil N

Karathanasis *et al.* (1980) and Bonfil *et al.* (1999) reported significant correlations between total soil N, residual mineral N, soil water content, soil organic matter and grain yield and protein content. Both the amount of residual mineral N in the root zone at planting and the amount of soil organic N mineralized during the growing season greatly affect the response of plants to applied N under field conditions. Stanford *et al.* (1977) have shown that residual N in the soil profile is an important source of N for plants, and should be accounted for in fertilizer recommendations. The position of residual N in the profile in relation to available water supply and root activity also influences plant response (Vlek & Craswell, 1981). In crop production, NO_3^- in the deeper soil horizons can be taken up relatively late in the season, resulting in enhanced grain protein. The upward movement of water through the soil profile due to evaporation and capillary flow can also result in NO_3^- movement from the subsoil into the rooting zone (Vlek & Craswell, 1981), but also depending on irrigation management leaching of these nitrogen forms beyond rooting depth can also occur.

Olson *et al.* (1976) indicated that residual soil mineral N in the soil is significant to grain production especially in non-humid areas where extensive leaching does not occur, and where fertilizer N has been used at modest to heavy rates in previous years. Differences in grain protein have also been related to differences in residual N levels in the soil rooting profile (Smika & Greb, 1973; Karathanasis *et al.*, 1980; Fiez *et al.*, 1994). For example, Smika & Greb (1973) found that soil nitrate in the profile at seeding was positively correlated with grain protein, where the protein content increased with an average of 0.15% for each kg/ha of NO_3 -N present in the soil. Fiez *et al*. (1994) also noted that pre-plant residual soil mineral N (0 - 152 cm) positively influenced grain protein, especially because this deep N is taken up later in the growing season when water is extracted from greater depths. Karathanasis *et al*. (1980) and Bonfil *et al*. (1999) reported significant correlations between total soil N, residual mineral N, soil water content, soil organic matter and grain yield and protein content.

The capacity of the soil to supply N to the crop is determined by a number of key factors (Goh & Haynes, 1986; Halvorson *et al*., 1987). These include:

- the amount of residual mineral N present in the potentially active root zone at planting or before crop growth commences,
- the amount of potentially mineralisable N present in the soil,
- the proportion of this potentially mineralisable pool of soil N that is mineralized during the growing season, and
- the amount of residual and mineralisable N that is immobilized or lost from the soil-plant systems by leaching or gaseous losses.

2.4 Plant growth components

Optimum management of N is necessary to reduce the environmental impact of agricultural practices and to increased profitability in crop production. Crop analysis (total N) has also been used to formulate N recommendations, since the plant is considered to integrate factors such as the presence of soil mineral N, the availability of this N, the weather and general crop management (Binford *et al.*, 1992).

2.4.1 Yield responses

Economic responses of crops to fertilizer N additions occur as increased yield or biomass yield, or grain quality improvement. The simplest response of plants to applied N, when N is the limiting factor, is a linear increase in dry matter production with rates up to the maximum application rate of N, staying constant thereafter or declining (Bock, 1984). The magnitude of response to applied N is dependant on the size of the available and potentially available pool of N in the soil, and the demand by the crop as determined by its potential dry matter production and minimum tissue N concentration (Olson & Kurtz, 1982).

In small grain crops, leaf area is typically increased by increasing levels of applied N (Yoshida, 1972). This is due to an increased number of tillers, leaves and increased leaf size and longevity. The potential photosynthetic capacity and rate of photosynthesis is raised, but so are respiration rates. Thus, the overall effect of applied N is an increase in the source capacity of the plant, while the number and size of the grains and their rates of growth determine the sink capacity (Yoshida, 1972):

Grain yield/ha = ears/ha x spikelets/ear x grains/spikelet x weight/grain

2.4.2 Nitrogen uptake and concentration

The quantity of N removed in the different components of the crop is usually the major determinant of fertilizer N requirement of that crop. This is because the yield and N uptake of modern crops is large in comparison with the N supplying capacity of most soils (Olson & Kurtz, 1982). Nitrogen deficiency is closely related to restricted chlorophyll synthesis, and it typically results in a reduction in plant growth. When soluble N reserves in plants are inadequate to sustain the N demand, breakdown of insoluble leaf proteins occurs (Haynes, 1986c). Yellow discoloration starts on the older leaves since N is translocated to younger leaves, and as the severity of the deficiency increases, the entire plant turns yellow, the older leaves turn brown and die, and plant growth ceases. By comparison, vigorous plant growth with a dark green colour results from an oversupply of N (Snowball & Robson, 1991).

The utilisation of N by higher plants involves several processes including, uptake mechanisms, storage, translocation, reduction and incorporation into organic forms (Moll *et al*., 1982). Under conditions of limited supply of N, remobilization of previously assimilated N can occur by breakdown of insoluble protein sources. Under these conditions, most of the N in wheat grain can be derived from remobilization, whereas under conditions where N uptake from the soil is possible during grain development, remobilization may be less than 50% of grain N. Plant uptake of N and resulting N concentration of plant material is linked to the specific plant developmental stage, N supply and subsequent redistribution of N within the different plant components. Nitrogen requirement is therefore related to total N removed by the crop (Osaki *et al*., 1991).

Plant analysis can provide an effective means of monitoring the nutritional status of a crop. If critical tissue concentrations are known, potential deficiencies can be identified before visual symptoms appear, and additional nutrients applied before yields are reduced (Vaughn *et al*., 1990). Typically, the N concentration of leaves and tillers is high during the vegetative stages and decreases rapidly as N is redistributed to reproductive organs from ear emergence to maturity (Osaki *et al*., 1991; Zhang *et al*., 2000). This results in decreases in total biomass and tiller and leaf N contents. The loss in biomass can be ascribed to losses due to leaf fall, translocation to grain, and increased respiration (Greenwood *et al*., 1987; Herwaarden *et al*., 1998a). Losses in tiller dry matter are commonly observed during anthesis/grain filling. This includes a sizable loss due to respiration, assimilate remobilization to the grain and premature senescence of tillers (Simmons, 1987; Austin *et al*., 1987). The N concentration of different plant biomass components decrease during the growing season due to the dilution effect of growth and biomass accumulation on plant N concentration (Jarrell & Beverly, 1981; Olson & Kurtz, 1982; Cox *et al*., 1985; Ellen, 1990; du Plessis & Agenbag, 1994). Loss of N from the plant from anthesis to maturity has been found in several studies (Wetselaar & Farquhar, 1980; French & Schultz, 1984; Greenwood *et al*., 1987), with losses within a range of 21 to 41% in winter wheat (Raun & Johnson, 1999). Total plant N and grain N contents at maturity also responded positively to applied fertilizer N.

The grain dry matter response to N addition often varies according to the growing season (Clark *et al*., 1990; Bulman & Smith, 1993). Several authors have found that the proportion of grain N derived from post anthesis N uptake is highly related to dry matter accumulation during grain filling, which is in turn related to available soil water (Clark *et al*., 1990; Bulman & Smith, 1993; Ma *et al*., 2006). Macduff & White (1984) and Echeverria *et al*. (1992) found reduced plant N accumulation of barley at harvest when compared to earlier samplings. They attributed this to a net translocation of N from the shoots to roots, or a loss of N from senescing tissues either through volatilization as $NH_{3,}$ or leaching by rain of soluble N compounds within the tissues. Bänziger *et al*. (1992) found that total N accumulation in both the whole plant and grains are generally more related to biomass production than to tissue N concentration. The increases in N accumulation, biomass production and potential yields depend on soil water and N availability. Asseng *et al*. (1998) found in their studies with wheat significant differences in tiller N concentration and accumulation at stem elongation and the beginning of grain filling. Higher tiller N concentrations contributed to the delay of leaf senescence and probably improved photosynthetic activity, and these combined effects may have helped to extend the life of the root system (van Keulen *et al*., 1989), extending further growth and accumulation of N (Smith & Gooding, 1996).

The plant is the ultimate genetic integrator of all environmental variables controlling N transformations and ultimately available N within the soil N cycle (Broadbent, 1981; Rice *et al.*, 1995). Crop analysis (total N) has also been used to formulate N recommendations, since the plant is considered to integrate factors such as the presence of soil mineral N, the availability of this N, the weather and crop management (Binford *et. al*, 1992). Crop N uptake can provide an estimate of N availability during the growing season, while N uptake by an unfertilized (N) crop can give an indication of net N mineralization in the field (Rice *et al.*, 1995). The advantages of this approach are the integration of field temperature, moisture and aeration conditions that can greatly influence N mineralization potential, and furthermore it can be adapted to include crop and soil management variables. Nitrogen uptake in unfertilized plots also includes the normal rooting depth of the crop and integrates spatial and temporal influences on N mineralization (Broadbent, 1981; Rice *et al.*, 1995). Optimum management of N is necessary to reduce environmental impact of agricultural practices and to increased profitability in crop production.

2.4.3 Nitrogen uptake and content of plants

Changes occur in dry matter and nutrient accumulation and in mass distribution among plant components of wheat plants with continued plant development (Bauer *et al.*, 1987). Wheat tissue N concentrations (in particular stem and leaf tissues) decrease during the growing season because of the slower rate of N relative to C assimilation (Harper *et al.*, 1987). Nitrogen concentrations of leaves are typically high during the vegetative stage, then decreases during the growing season, with large amounts of N in the leaves and stems redistributed to reproductive organs during maturation (Osaki *et al.*, 1991).

The basic principle in the use of plant nutrient analysis is that the chemical composition of a plant reflects the interaction of nutrient supply and plant growth at that point in development (Martin & Matocha, 1973). Even though nutrient concentration of plant tissue decreases, the total accumulation of this nutrient as calculated by the product of concentration and dry matter yield may increase significantly. This indicates that plant growth had proceeded more rapidly than nutrient uptake (Jarrell & Beverly, 1981). These authors also noted that the nutrient concentration of plant tissue is a single-point measurement resultant from plant growth history and in particular, integration of the processes of nutrient uptake, transport and dry matter accumulation. The ‘dilution effect’ is referred to in plant nutrition studies to explain the results that arise when the concentration of an element is decreased (or increased - concentration effect) due to a change in plant growth induced by environmental conditions. This causes changes in the nutrient concentration in the plant as a function of time, due to increased dry matter accumulation.

Plant tissue analysis at a specific growth stage and under optimal environmental conditions can provide an effective means of monitoring the nutritional status of the crop. Reliable N recommendations for wheat relying on plant analysis must be based on accurate critical nutrient concentration levels (Vaughn *et al*., 1990), but the total nutrient uptake and dry matter yield must also be considered (Jarrell & Beverly, 1981). The measurement of organic N (total tissue N analysis) reflects the cumulative effect of N supply to the plant (Tucker, 1984), necessitating whole plant samples when total N uptake is part of fertilizer use efficiency or N balance studies.

Young plants contain higher concentrations of nutrients (especially for N, P, and K) than older plants (Jarrell & Beverly, 1981), depending on the relative mobility of the specific nutrient in question. When a growth-limiting element is supplied, the relative rate of dry matter accumulation can increase more rapidly than rate of nutrient accumulation, resulting in lower final nutrient concentrations of treated plants (Jarrell & Beverly, 1981).

Furthermore, the remobilization and redistribution of N within the plant, causes changes in the N concentration of different plant parts over time. This causes difficulties in determining optimal N status of plants through analysis of plant parts. Several authors have suggested the use of total aboveground dry matter at different growth stages for determining the critical N concentration (Olson & Kurtz, 1982, Tucker, 1984; Goh & Haynes, 1986). This point differs with the kind of plant, plant part, position on the plant, stage of growth, or plant product specific to a particular plant (Tucker, 1984).

Results of a study by du Preez & Bennie (1991) on the concentration, accumulation and uptake rate of macro nutrients of irrigated wheat confirmed the decrease in N, P and Ca concentrations in biomass as the growing season progressed, due to the dilution effect of plant growth on nutrient concentration. These authors calculated a total N uptake of 213.7 kg N/ha, with 99.9 kg N/ha accumulated in the grain, which corresponds to a NHI of 0.467. They also found that the accumulation of N at harvest was more than the fertilizer N applied, indicating the supply of soil mineral N via mineralization during the growing season. Maximum nutrient uptake rates increased with the age of the crop, and for N the maximum uptake rate was found at 70 to 80 days after planting, corresponding with the late tillering up to flag leaf growth stages.

Bulman & Smith (1993) stated that cultivars are known to vary in leafiness and tillering ability, with leaf tissues generally having higher N concentrations than stem tissues.

Synthesis, translocation, partitioning and accumulation of photosynthetic products within the plant are controlled genetically, but influenced by the cropping environment. Leaves, other green tissues and organs of plants that produce photosynthates are called sources. Organs or tissues that receive these products temporarily store them, and release these products at a later stage to other sites are also called sources (Snyder & Carlson, 1984). All sites within the plant, which utilizes photosynthetically derived products, either *in situ* or after receiving the products, are called sinks. There is a close relationship between net photosynthesis and crop yield, as well as the need for improved translocation (from biomass to developing grain) and larger sink capacity (ear size/number and kernels per ear). Translocation requires metabolic energy and chemical gradients for moving compounds from the source to the sink. Snyder & Carlson (1984) found that as grain matured in wheat, its sink strength or ability to accumulate photosynthates increased as compared to other competing sinks. This sink capacity (number of ears and grains/m^2) is significantly influenced by the harvest index (ratio of grain yield to total above ground biomass yield at harvest) of a cultivar.

Greenwood *et al*. (1987) found that approximately 80% of the total aboveground N content of wheat plants was in the grain irrespective of cultivar or experiment, while Wetselaar & Farquhar (1980) reported a range of 65-75% in research carried out on earlier released wheat cultivars. Due to the limited sink size (lower yield potential because of lower grain number) the increased source of available N (total biomass N content) could not be completely transferred to the grain, resulting in high N concentrations in the residue.

Total plant uptake of N would be best expressed by total biomass N. However, N in roots, root residues and root slough materials are difficult to measure. For this reason, total above ground N is the estimate of plant N uptake most commonly used. Typically, N uptake by field crops involves a period of very slow accumulation followed by a rapid increase that coincides with rapid plant growth. Uptake rates of between 3 and 5 kg N/ha per day can occur during this rapid uptake phase. This also results in high N concentrations in young seedlings, and there is a characteristic decline in the N concentration as the plant ages and accumulates dry matter (Tinker, 1978; Goh & Haynes, 1986). The response of the crop (grain yield and grain protein concentration) to applied N also depends on the redistribution of N within the plant, as there is remobilization and translocation of N within the plant during grain development.

2.4.3.1 Grain protein concentration

The predominant positive impact of N on crop quality is in its enhancement of the total N content of crops, and in grain crops specifically the protein concentration of grain (Olson & Kurtz, 1982). Grain protein typically increases with increasing rates of N above those needed for optimum yields (Jackson *et al*., 1973). Delayed applications of fertilizer N also tend to increase grain protein concentration, especially application at the flag leaf to anthesis growth stages (Loffler *et al*., 1985; Jenner *et al*., 1990). Soltanpour *et al*. (2001) stated that grain protein concentration increased with increasing N fertilizer applications, but decreased with increased yield potential, especially if the amount of N fertilizer applied was not proportionately increased.

Application of post-emergence N has been successfully implemented on irrigated wheat to manipulate grain protein and yields (van Rensburg, 1996; Karamanos *et al*., 2005). The concentration of protein in wheat grain is also influenced by the supply of N via the soil, the interaction with soil water availability, temperature, cultivar and timing of N application (Karamanos *et al*., 2005). These authors also found in their study that in contrast to yield, grain protein was influenced by both N applied at seeding and post-emergence. The impact of N applied at seeding was greater when soil organic matter levels were below 5%. They also confirmed that grain protein does recover once the maximum yield potential provided by the cultivar and the agroecological conditions have been reached. Detrimental effects of excessive N availability on wheat growth include lodging, delayed maturity, shrivelled kernels with a abnormally high protein concentration and increased susceptibility to diseases, all of which lead to reduced baking quality (Halvorson *et al*., 1987). Adequate N fertilization is necessary to produce high yields of wheat and to increase the quality (grain protein concentration).

High levels of protein are important for superior wheat flour and baking characteristics (Feil, 1997), but protein concentration is not the only factor that determines the baking quality of the flour. The importance of the relative composition of grain protein, i.e. gliadins, glutenins and other fractions, has also been emphasized. The specific proteins that make up the four protein fractions of wheat are genetically determined. However, the proportions of these specific proteins may be affected by environmental factors and soil fertility, especially the level of available N. It was noted that increasing the protein concentration by N fertilization frequently decreases the general nutritional content of wheat, mainly because of the increase in the prolamin fractions at expense of the lysine protein fraction (Deckard *et al*., 1984), although this effect is variable.

The environmental and genetic variation in grain protein is described by Kramer (1979), and the implications to overcome the negative correlation between grain yield and grain protein concentration is reviewed by Feil (1997). The grain protein concentration is an important component of the quality of the produced grain, and the trait most commonly used to measure it, since it is considered to be of great importance for both human nutrition and bread quality (Slafer *et al*., 1990). Demands for nutrition take into account high grain protein concentrations, economic and ecological demands for reducing N input without decreasing yield. Farmers everywhere are under increasing pressure to produce wheat grain that meets specific market and nutritional requirements, while efficiently utilizing inputs to ensure that economic and environmental standards are met.

Protein-rich grain crops have a high demand for N during grain filling, and mobilization of soluble N and breakdown products of insoluble N reserves in the leaves can be an important source of grain protein (Novoa & Loomis, 1981; Haynes, 1986c). With an adequate supply of N, protein losses during remobilization are high only in older leaves, but with a low supply of N, mature leaves lose protein linearly with age (Novoa & Loomis, 1981). Under extreme N deficiency, protein levels of very young leaves of wheat are reduced and most of the N in wheat grain is derived from remobilisation of N from the vegetative tissues (Evans *et al*., 1975). Under conditions where N absorption from the soil is possible during grain development, remobilization may be the source of less than 50% of grain N (Evans *et al*., 1975).

The contribution of post-anthesis N accumulation to grain N content was generally found to be low, since wheat accumulates around 85% of its total plant N before anthesis (Creagan & van Berkum, 1984), and this N is remobilised to the ear during grain filling (Dalling, 1985). The capacity of the crop or grains to accumulate N (Dhugga & Waines, 1989), root senescence (Hageman, 1979) and N and water availability during the later growth stages have been suggested to be limiting factors for improving the post-anthesis accumulation of N in wheat (Ma *et al*., 2006). In general, the response of grain protein to higher rates of N also depends on factors that affect N supply to the plant and accumulation of N in the grain. In turn, the N supply is affected by initial levels of soil fertility or total available N, previous cropping and soil water content (Bole & Dubetz, 1986; Ma *et al*., 2006). Available N increases plant N accumulation by increasing leaf area and leaf N concentration (Orphanos & Krentos, 1980; Bulman & Smith, 1993), and leaf area duration (Novoa & Loomis, 1981). Lower grain protein often is the result of relatively higher yield responses to N application, resulting in the dilution of grain protein because of the reduced pool of available N (source) in relation to the increased yield (sink), again necessitating additional post flag leaf applications of N.

2.4.3.2 Environmental conditions

The response of crops to N can be modified and affected by environmental factors from season to season (Keeney, 1982). Good farm management practices are essential for optimum yield responses of wheat to fertilization. These practices include; proper irrigation management, use of high yielding cultivars, use of soils suitable for wheat production, disease, weed and insect control, appropriate crop residue management and crop rotations, and proper seeding and harvest methods.

Increased N fertility can stimulate deeper rooting of wheat, making a greater quantity of stored soil water available to the plant, thereby reducing potential water stress. However, larger aboveground biomass stimulated by increased N availability results in greater transpiration demands (Ritchie & Johnson, 1990). Thus, if sufficient water reserves were not available, greater water stress in high N treatments would occur, possibly during the later critical crop development stages, thereby reducing the yield. Continuous cereal cropping, without N inputs from fertilizers or legumes has led to widespread deficiency of N in wheat (Doyle & Holford, 1993). This has occurred on soils previously regarded as high in available N and which have produced high grain protein wheat for relatively short periods (< 40 years) of wheat production. The utilization of N by the crop can be influenced by planting date, plant nutrition other than N, soil pH, availability of water, variety, light, temperature and other biological conditions like weeds, insects and diseases.

Nitrogen applications for adequate N availability early in crop development promotes tillering, leaf growth, and potential grain number. However, ultimate responses to N are modified by environmental conditions, in particular temperature and rainfall, as well as inherent and continued soil N fertility (Jenner *et al*., 1990). Characteristic of responses to N fertilizer in semi-arid environments is the large season-to-season variability, which is mainly due to the unreliability of seasonal rainfall and soil water availability (Taylor *et al.,* 1974; McDonald, 1989; Ma *et al*., 2006). The importance of rainfall emphasizes the interaction between water availability (soil water and amount of rainfall) and N responses measured as plant N concentration and accumulation, yield, and quality of the grain. Because N is a relatively mobile element in soils, it is transported to roots mainly by mass flow. Lowering the supply of soil water will reduce response to N fertilizer both directly, by reducing flow of N to roots, and indirectly by reducing growth of the crop and thereby demand for N (Haynes & Goh, 1978; McDonald, 1989).

Environmental factors also markedly influence dry matter accumulation and it's partitioning (Snyder & Carlson, 1984). Water and nutrient stress result in lower photosynthetic rates, and alter partitioning of synthesized products (Snyder & Carlson, 1984). The effect of water stress on dry matter accumulation in cereal grains depends on the time and intensity of stress (Donald & Hamblin, 1976). The severity of water stress and the rate at which it develops depends on the amount and distribution pattern of rainfall during the growing season as well as on soil type. The critical phase of growth when water stress reduces grain yield is the period from anthesis to grain physiological maturity. To obtain high grain yields, the stress level in the crop should be minimized during this stage (McDonald, 1989).

High temperatures (> 30℃) during the post floral stage decrease the total amounts of assimilated products transported to grain and generally produce lower yields (Yoshida, 1972; Spiertz, 1974; Bhullar & Jenner, 1986; Jenner *et al*., 1990). Elevated temperatures during the post anthesis stage may cause premature cessation of starch deposition in the endosperm of developing grain, even in well-watered crops (Bhullar & Jenner, 1986). While the rate of starch deposition may be faster under high temperatures, it does not compensate adequately for the shortened duration, so the total amount of starch deposited is less, thereby leading to lowered yields (Yoshida, 1972). On the other hand, deposition of protein appears to be largely unaffected by elevated temperatures, and an increase in grain protein percentage can therefore result (Bhullar & Jenner, 1986; Smith & Gooding, 1996).

The response to mild water stress in the reproductive phase of growth is similar to the response to elevated temperatures. Stress induced by a water deficit typically results in premature yellowing of the leaves implying the induction of premature senescence (Jenner *et al*., 1990). The development of all plant organs is enhanced at high temperatures; so accelerated grain development is accompanied by hastened senescence of leaves (Jenner *et al*., 1990).

Generally, assimilates contributing to grain yields are derived from current photoassimilate, but when conditions such as drought occur, currently available assimilate supplies are reduced, and the plant relies more heavily on previously stored assimilates for grain filling (Gallagher *et al*., 1976; Simmons, 1987). If demands on stored assimilates are excessive, they are remobilised from various vegetative plant parts inducing senescence, and are translocated to the grain, providing nutrients, including N, for grain development. Herwaarden *et al*. (1998b) suggested that one of the consequences of soil water depletion or lack of sufficient soil water at anthesis is a reduced assimilation rate during grain filling. In wheat, grain size is variable, so that the influence of environmental factors during grain filling can directly influence yield potential by modifying the grain size (Yoshida, 1972; Jenner *et al*., 1990). Simmons (1987) suggested that between 70% and 90% of the grain yield is derived from photoassimilate produced after anthesis, by the flag leaf, penultimate leaf, peduncle and ear.

Jarrell & Beverly (1981) listed the following factors that can lead to a decrease in dry matter accumulation of crops; a decrease in photosynthesis, increases in respiration, reduced photosynthate translocation, limited water availability, accelerated senescence, hastened maturity, decreased growth period, and greater disease-, pest-, or temperature related losses of yield potential. High temperatures during grain filling lead to an increase in leaf senescence, which reduced the accumulation of carbohydrates more than that of N (Spiertz, 1974; Bhullar & Jenner, 1986; Jenner *et al*., 1990). Higher temperatures during grain filling can reduce the duration of grain growth and limit the maximum size of the grain (Smith & Gooding, 1996). Nitrogen translocation is however less retarded and this can lead to increased grain protein content (Smith & Gooding, 1996).

The ability to efficiently remobilise previously accumulated photosynthates to the grain influences the harvest index and grain yield at maturity (Gent & Kiyomoto, 1989). Up to one-half of the photosynthates fixed before anthesis can be lost from wheat plants by maturity. Rainfall later in the growing season may cause N dilution in the grain by extending leaf life and maintaining photosynthesis, and therefore carbon assimilation (Smith & Gooding, 1996). This response is due to favorable soil water conditions delaying senescence and physiological maturity, allowing translocation of photosynthates to developing grain over an extended period. Doyle & Holford (1993) found a more complete transfer of N from biomass to grain in dry years (on average lower in-season rainfall), than in wetter growing seasons (mean to above-mean rainfall in cropping season). They stated that translocation of N to developing grain is less retarded by relatively dry conditions than uptake into biomass. Thus, there was a relatively greater transfer of N from biomass to grain in dry years (Doyle & Holford, 1993).

The onset of leaf senescence after anthesis results in transport of N to the grain as found by Herwaarden *et al*. (1998b). They also found a trend for reduced remobilization of N from leaves subjected to high temperatures, due to desiccation and sudden death of distal portions of green leaves making those areas of leaf inaccessible to catabolism by the plant. Thus, water stressed crops often have a high final leaf N concentration (Clark, 1983; Herwaarden *et al*., 1998b). The relationship between yield and grain protein percentage across soil N levels can vary from negative to positive, depending on the specific environmental conditions (Deckard *et al*., 1984).

2.5 Fertilizer N recommendations

Nitrogen is one of the most important minerals that determine crop productivity. The evaluation and understanding of the pattern of N uptake and its distribution in the crop throughout the growing season can be used to predict N requirements for improving N fertilizer management (Bauer *et al*., 1987; Baethgen & Alley, 1989b). Knowledge of plant nutrient concentrations in relation to plant development stage is valuable as it provides information for management decisions relative to timing of nutrient applications to avoid the occurrence of deficiency or surplus situations (Bauer *et al*., 1987).

High N use efficiency by crops should be expected when the N availability and mobilization matches the crop’s needs throughout the growing season. Variations in climate and cultural conditions influencing plant growth, mineralization and N uptake can result in varying N availability indices from year to year, making the accurate prediction of fertilizer N requirement difficult. Methods of monitoring soil and plant-N status have been developed to alleviate these difficulties. These methods include both direct and indirect measurements of soil and plant mineral N and plant response to fertilizer (Gerik *et al*., 1998). For soils, direct methods include the measurement of soil nitrate and ammonium, soil organic matter, and N mineralization. For plants, direct methods include measurements of total plant N, stem nitrate concentration and nitrate reductase activity. Indirect methods include measurements of leaf chlorophyll content and the use of physiologically based crop models (Gerik *et al*., 1998).

In compiling fertilizer N recommendations, the N requirement of the crop is important as influenced by yield, N content and efficiency of N uptake from the soil, and the availability of N fertilizer to supplement soil N supply as influenced by immobilization, leaching and gaseous losses (Broadbent, 1981; Rice *et al*., 1995). For fertilizer N recommendations, the N requirement of the crop is important (Legg & Meisinger, 1982; Olson & Kurtz, 1982), with the N requirement under field conditions influenced by:

- crop requirement as determined by yield and N content,
- the effectiveness of the crop to recover available mineral N from the soil profile as affected by growth stage and root development,
- availability of N fertilizer when added to supplement soil N supply as influenced by immobilization, leaching and gaseous losses.

The availability of residual N to the crop is normally considered equal to that of fertilizer N. However, Habey *et al*. (1983) concluded that residual soil NO_3^- was only one-third as efficient for grain production as fertilizer N, irrespective of water supply. They concluded that further research is needed to estimate substitution rates of soil mineral N in different soil layers for fertilizer N if the recommendations for fertilizer applications are to be improved.

2.6 Nitrogen use efficiency (NUE)

The NUE of a crop is a function of the genetic constitution and the environment in which it is grown, determined by climate, soil, and management, since all these factors control the rate of dry matter production (Olson & Kurtz, 1982). Nitrogen use efficiency is therefore a complex term with many components. In addition, a great degree of compensation takes place among the components (Ladha *et al*., 2005). To quantify NUE, the term mostly used is a ratio of an output (biological or economical yield) to the input (N supply or fertilizer), based on an incremental or cumulative base (Bock, 1984). Biological yield can include aboveground biomass or total plant N, while economic yield includes grain yield or total grain N. Nitrogen use efficiency (NUE) of wheat is considered from the three interrelated points of view: agronomy (in terms of grain yield produced per unit of N supply), environment (possible contamination of ground water, eutrofication of surface waters, or ozone depletion by release of N_2O) and economics (maximization of farmers' income) (Raun & Johnson, 1999). From the agronomic perspective, NUE has usually been considered with respect to the relationship between yield and N rate (yield efficiency), recovered N and N rate (N recovery efficiency) and the yield and recovered N (physiological efficiency). The different NUE components can generally be defined as the maximum economic yield produced per unit of nutrient applied, absorbed or utilized by the plant to produce grain or biomass.

In the literature, NUE components have been defined in several ways (Fageria & Baligar, 2003). The efficiency of N use in wheat can be considered in terms of the following efficiency components (Moll *et al*., 1982; Bock, 1984; Craswell & Godwin, 1984; Doyle &

Holford, 1993; Ortiz-Monasterio *et al*., 1997), where YF and YC are the grain yields of the fertilized (F) and unfertilized (C) plots, NF and NC are the N uptake and accumulation in the grain and biomass (kg/ha) of the fertilized and unfertilized plots respectively, and *F* is the quantity of fertilizer N applied (kg/ha) (McDonald, 1989).

- **Agronomic efficiency (kg/kg) = (YF-YC)/*F* =kg/kg**

The amount of grain produced relative to the amount of fertilizer N applied may be used to estimate NUE, and this ratio (kg grain/kg N) has been defined as agronomic efficiency (NAE) (Ladha *et al*., 2005; Stevens *et al*., 2005). The NAE estimates the overall efficiency of the production system and is the product of apparent recovery and physiological efficiency (Craswell & Godwin, 1984). As this calculation subtracts the yield of the control from the yield of the N treatment plot, this difference method assumes that N fertilization has had no additional positive or detrimental effects on plant uptake of soil N, and that all other agronomic factors are considered equal between the respective treatments (Stevens *et al*., 2005). One weakness of evaluating or predicting N fertilization application rates by NAE is that the contribution of mineralization of organic soil N is overlooked (Stevens *et al*., 2005), especially in long-term experiments where mineralization rates between fertilized and unfertilized plots are different. However, Stevens *et al*. (2005) concluded that the difference method is most appropriate for fertilizer N experiments that are newly established and where variability among plots in soil mineral N availability is minimal. Van Rensburg (1996) calculated in a South African study values of 12-46 kg grain yield/ha per kg N applied (17.6 kg/kg N on average) at increasing irrigation water application treatments.

- **Apparent recovery efficiency (%) = (NF-NC)/*F* * 100 = %**

The apparent recovery (NRE) estimates the efficiency of the crop in utilizing applied N fertilizer and is therefore affected by climate, which influences both soil mineral N availability and crop growth. The NRE values were calculated as the total N recovered in the above ground biomass at the fertilized treatment minus the N recovered in the respective unfertilized control, divided by the rate of N applied and is expressed as a percentage. Although this calculation does not include the N contained in the root system of the plant, it nonetheless is a usable indication of the recovery efficiency. Field experiments indicated that the recovery of applied N under average field conditions is often no greater than 50-60%, but with efficient N application, timing and placement it would be possible to recover 70-80% of applied N (Legg & Meisinger, 1982). Van Rensburg (1996) calculated a recovery percentage of 64% in a study on a South African wheat cultivar. In general, the amount of fertilizer N recovered by crops increases with application rates, while the recovery efficiency declines with increasing rates of application, although this varies with climate, soil and management practices (Rao *et al.*, 1991).

- **Physiological efficiency (kg/kg) = (YF-YC)/(NF-NC) = kg/kg**

Physiological efficiency (NPE) is a measure of the ability of crops to utilize N in the synthesis of grain yield and is affected by environmental stresses and the plant genotype. The NPE values were calculated as the yield of the fertilized treatments minus the yield of the unfertilized control divided by the N measured in the aboveground biomass of the fertilized treatments minus the N measured in the biomass of the unfertilized control. Van Rensburg (1996) calculated a NPE value of 27 kg/kg N uptake in a study on a South African wheat cultivar.

However, NUE components can be subdivided into multiplicative components that identify soil and plant processes contributing to overall N use (Moll *et al.*, 1982). This analysis can be expanded to examine management impacts on the different NUE components, and can be used to identify inefficiencies that could be improved with altered management or genetic selection (Huggins & Pan, 1993). Ortiz-Monasterio *et al.* (1997) proposed the following additional NUE calculations: (crop N supply calculated as the soil mineral N content at planting plus the applied fertilizer treatment (kg N/ha)). These calculations include soil mineral N at planting and applied fertilizer N, assuming no losses of N from the soil-plant system. The beneficial effect of applied N at the N treatments (bigger root system and increased N mineralization) and therefore better use of available soil N are part of the N response calculated.

- Nitrogen uptake efficiency = plant N accumulation/crop N supply *100 = %; this is the percentage of the available N supply (soil and fertilizer) that is taken up into the plant biomass.

- Nitrogen use efficiency (biomass) = total dry matter accumulation/crop N supply = kg/kg N

- Nitrogen use efficiency (grain yield) = grain yield/crop N supply = kg/kg N

- Nitrogen utilization efficiency (biomass) = total dry matter accumulation/total plant N accumulation = kg/kg N

- Nitrogen utilization efficiency (grain yield) = grain yield/total plant N accumulation = kg/kg N

- Nitrogen harvest index = Grain N accumulation/total plant N accumulation; Nitrogen harvest index (NHI) was calculated as the N content measured in the grain (kg N/ha) divided by the total aboveground N in the biomass (grain plus residue). Percentage N concentration (%) was determined for grain and residue samples. Grain N and residue N content was calculated as the respective N concentrations multiplied by the yield and biomass measured.

The impacts of management practices on the processes involved in NUE, such as N uptake, N utilization and N retention in the cropping system can be used to identify inefficiencies that could be improved by altering management or by genetic selection (Huggins & Pan, 1993). However, in view of economic and environmental concerns, more efficient ways of fertilizing wheat crops with N should be investigated, since the encouragement of high N inputs to combine high yields with high quality increases the risk of nitrate leaching, N volatilization and support energy requirements, without necessarily giving a consistent benefit to the end user (Gooding & Davis, 1997). Excess N is often applied as insurance, because farmers are overly optimistic concerning expected yields and yield goals, although du Plessis & Agenbag (1994) calculated decreased N utilization values at high N fertilization levels in a Mediterranean climate in South Africa. Because of this, the affordability of N in the developed world has led to misuse and over application. The same does not always hold true in the developing world, where access to fertilizers is limited. The goal for subsistence farmers in remote areas is economic survival, and not necessarily preservation of the environment (Raun & Johnson, 1999). Rational applications of N to avoid excessive fertilization and the use of cultivars that efficiently use N sources have been proposed, among other strategies, as being of prime importance for NUE.

Many authors have reported that N use varies among cropping systems, which can lead to different responses of yield patterns to fertilizer N. Differences in genotype reactions, among other factors have also been reported (Bänziger *et al*., 1992). The cycling of N in growing plants and the recovery efficiency of N in the plant-soil system had been a topic of considerable interest over the years. Researchers have found that not all of the soil and fertilizer N measured at planting can be accounted for at the end of a growing season. Research has also suggested that N can be lost from soils in volatile forms as ammonia, dinitrogen, nitric oxide, nitrogen dioxide and nitrous oxide (Haynes, 1986a; Harper *et al*., 1987). Losses from the plant may also occur and these have been shown to include gaseous NH_3 (Farquhar *et al*., 1983). In addition to these direct losses of N, applied fertilizer N may also become unavailable to the plant due to microbial immobilization, particularly in management systems with high amounts of organic residue in the upper soil layers (Harper *et al*., 1987).

2.6.1 Genetic variability for NUE

Comparative studies of wheat cultivars from different breeding eras revealed that modern cultivars often out-yield earlier released cultivars. However, to obtain a simultaneous improvement in grain yield and grain protein concentration by breeding is considered challenging because of the negative relationship usually found between these traits (Slafer *et al*., 1994; Lawlor, 2002). Protein synthesis cannot continue without N, therefore an adequate supply of N is a prerequisite for high protein yields.

The potential for breeding for N use efficiency in crops is dependent on the genetic variability present in the species for the trait(s) that determine efficient N utilization, and the development of procedures to accurately measure components that reflect N use by the plant (Sherrard *et al*., 1984). Genetic variability for NUE in wheat has been reported (Ortiz-Monasterio *et al*., 1997). In the semi-dwarf cultivars originating from CIMMYT the increases in yields have been associated with gains in both NUE components: uptake and utilization efficiency at the medium to high levels of N fertility, and only with uptake efficiency under low N fertility. This suggests that the level of N in the soil plays an important role in the genetic expression of uptake and utilization efficiency of N in wheat (Ortiz-Monasterio *et al*., 1997).

Differences between species and genotypes in their ability to absorb, translocate, and utilize soil and fertilizer N can be ascribed to variations in plant growth rate and morphology, as well as the capacity for uptake and metabolism. High yielding cultivars are characterised by rapid growth rates resulting in high dry matter production per unit land area that must be met by an adequate supply of N (Bänziger *et al*., 1992). Genotypes also differ in their capacity to produce dry matter at a given level of N supply (Bänziger *et al*., 1992). They also vary in their capacity to absorb, translocate and partition N within the plant. For grain crops, this is important since remobilization of N from the tillers and leaves is an important source of grain N and hence significant differences in NHI among cultivars have been detected, although responses have been varied (Clark, 1983). Field experiments have shown that genetic variability in N uptake and partitioning efficiency exists in small grains (van Sanford & MacKown, 1986), while du Plessis & Agenbag (1994) found that older South African irrigated wheat cultivars (Palmiet and SST 66) did not differ in their ability to utilize N, but differed in S uptake.

Genotypic variation has also been reported for N utilization efficiency expressed as the ratio of grain yield to total plant N but variation in grain yield is rather explained by N uptake than N utilization (van Sanford & MacKown, 1987). Genotypic variability was found for N accumulation and/or remobilization, therefore, an associated increase in grain yield and grain protein seems feasible (Bänziger *et al*., 1992). The environmental and genetic variation in grain protein concentration was described extensively by Kramer (1979) who also discussed breeding methods to alleviate the negative yield-protein concentration relationship.

The physical constraints imposed by soil on roots are substantially different from those imposed on the aboveground fraction of the plant. Measurements of root distribution of growing plants as a function of distance from the surface shows a pattern that is simply described as a logarithmic decrease in root density with distance from the soil surface, with this logarithmic distribution moving downwards as the plant grows (Andrew, 1987). The root distribution of a plant is primarily governed by its genome, which determines the morphology of its root system (Andrén *et al*., 1991). Within the genetic restraints, root distribution is also governed by availability of nutrients and soil water content as well as the penetration resistance of the soil (Scott-Russell, 1977). In general, roots grow rapidly in those parts of the soil that are rich in needed resources, which thus become efficiently exploited. Therefore, it can be assumed that root density will be positively correlated with the availability of scarce resources. As the root system grows and increasingly exploits the resource, the initial positive correlation should weaken and may even become negative (Drew, 1975).

The differential response of cultivars to N management could also be linked to their specific N requirements at certain stages of plant development during the growing season. Sufficient N is supplied to the grains through a greater remobilization of nitrogenous compounds from the vegetative organs to the grains or by means of a greater uptake by the root system. It is postulated that the above-mentioned process could be supported by genetic means, thereby increasing the proportion of plant N that is deposited in the grain as protein. The NHI (proportion of seed N to total biomass N) is considered a measure of how efficiently a plant utilizes acquired N for the production of grain protein. Depending on climate, cereal species, cultivar and management techniques, 40-90% of total biomass N is stored in the grains. This suggests that it is unlikely that grain protein yield can be increased by genetically improving partitioning efficiency (Feil, 1997). Another possibility for enhancing the amount of N in the plant is to breed for higher N uptake or to reduce losses of N from the plant.

The successful commercial production of available wheat cultivars thus depends on sound N fertilization guidelines in general. However, specific cultivar responses to N management and therefore N requirements vary according to growth patterns and yield potential development. Management aimed at achieving high yields with acceptable grain quality must therefore be adapted to the specific cultivar.

2.6.2 Agronomic and physical improvement for NUE

Bock (1984) reviewed the physical and agronomic potential and limitations for improved NUE. The author listed N recovery (maintaining N in forms available to plants and recovery of these available forms by the plant), physiological efficiency of a crop, yield versus quality aspects of a crop, and fertilizer N management as areas for possible improvements.

As a general trend, grain yields increase with an increase in total N uptake and genotypes can produce different grain yields with the same N uptake (Ladha *et al*., 2005). Harvest index (HI) indicates the translocation efficiency of dry material to grain, while the total biomass or biological yield indicates the potential volume for uptake and storage of N. Much of the progress in improving NPE of crops has been associated with improvements in HI rather than in photosynthetic efficiency. However, cultivars with a greater N use efficiency, which is not associated with a higher HI, will have lower grain protein concentrations. This reduction in grain protein has been associated with a higher NPE of wheat (Ladha *et al*., 2005). The relative importance of both N uptake and NUE may differ among production systems, making it necessary to select and evaluate for NUE under both low and high N levels (Ladha *et al*., 2005). This allows breeders to identify lines that perform well under N deficient conditions and lines that respond well to high N availability conditions.

Nitrogen harvest index (NHI) is the ratio of N in the grain to the total amount of N stored in the biomass at harvest, and van Rensburg (1996) calculated an average value of 0.81 for a South African irrigated wheat cultivar. According to Paccaud *et al*. (1985) total N uptake and NHI are considered the two main components of N use efficiency. These authors reported that increased levels of N application decreased NUE, and that NUE was therefore the highest with low levels of applied N. Increasing grain protein concentration by applying higher rates of N fertilizer is relatively inefficient, as NUE decreases with increasing N level (Raun & Johnson, 1999).

Wheat grain protein was shown to be genetically controlled and significant genotypic differences in this characteristic have been noted. It was also found that grain protein is strongly affected by environmental factors and agricultural practices like N fertilization and soil water management (Mihaljev & Kovacev-Djolai, 1978). The use of diallel analysis lends itself to detailed genetic analysis, and it can provide insight into the nature of genetic variances and the magnitude of its components (Sayed, 1978).

2.6.2.1 Combining ability

Estimation of genetic variance components is an important part of quantitive genetics. A generic mating design is often required to reach this goal, including the various types of diallel mating designs (Griffing's mating designs) (Griffing, 1956). Usually, the ANOVA approach is used to estimate these genetic variance components (Wu *et al*., 2006).

Combining ability has been defined as the performance of a line in hybrid combinations (Kambal & Webster, 1965). Assessment of the combining ability could be useful to define the contribution of a genotype to the performance of its progeny, because it defines the ease with which progress through selection can be made. Gene action is divided into two categories (Sprague & Tatum, 1942; Rojas & Sprague, 1952) namely general combining ability (GCA) and specific combining ability (SCA). They defined GCA as the average performance of lines in a number of hybrid combinations and that of SCA as deviations of certain crosses from expectations based on the average performance of lines involved.

General combining ability is largely due to additive gene effects and higher order additive gene interactions, while SCA is largely a function of non-additive dominance gene effects and other types of epistasis (inter-allelic gene interactions) as well as genotype x environment interaction (intra-allelic interaction) (Griffing, 1956; Cukadar-Olmedo *et al*., 1997). Thus, significant values of SCA could be interpreted as indications of the predominance of non-additive gene effects caused by dominance and epistasis (Kambal & Webster, 1965).

Le Gouis (2002) studied seven wheat cultivars in a 7x7 diallel over two years with and without N fertilizer application of 150 kg N/ha. He found high mid-parent heterosis for grain yields that were related to above ground biomass, although the magnitude of response varied over the tested years. However, the GCA and SCA effects were always significant. The GCA x N level interaction indicated different parental contributions at low or high N levels.

The ratio of GCA:SCA can reveal the nature of genetic variance. Should the GCA variance be greater than SCA variance, a higher ratio is eminent indicating the prevalence of the additive genes versus the non-additive components (Sayed, 1978). Mihaljev & Kovacev-Djolai (1978) found highly significant SCA and GCA values in a study on combining ability of wheat for grain protein content, and postulated that improvement in F_1 commercial hybrids could be achieved by selective choice of parents carrying the dominant gene for high grain protein content. Le Gouis (2002) found a range in GCA:SCA ratios of 3.6 to 14.8, with a tendency of higher ratios when N fertilizer was not applied. This indicates that the choice of parents will be dependent upon the N level under which new hybrids will be grown.

2.6.2.2 Heritability

Heritability is a measure of the correspondence between breeding values and phenotypic values (Jones, 1986; Falconer & Mackay, 1996). Allard (1960) used the term heritability to specify the genetic portion of the total variability. Heritability is therefore a measure of the ability of the plant breeder to recognise genetic differences among cultivars, and genetic variance indicates the potential for improvement in a population. Successful selection is dependent on a high heritability of characteristics.

Heritability can be expressed as broad-sense or narrow-sense values. Broad-sense heritability (h^2_b) is the ratio of the genotypic variance including additive dominance and epistatic variance to the phenotypic variance ($\sigma^2_g/\sigma^2_{ph}=\sigma^2_g/(\sigma^2_g+\sigma^2_e+\sigma^2_{ge})$), it expresses the extent to which individuals' phenotypes are determined by the genotypes. Narrow-sense heritability is a ratio of the additive genetic variance to the phenotypic variance (σ^2_A/σ^2_{ph}), it expresses the extent to which phenotypes are determined by the genes transmitted from the parents. Heritability in the narrow-sense determines the degree of resemblance between relatives (Falconer & Mackay, 1996), and measures the relative importance of additive portion of the genetic variance that can be transmitted to the next generation of offspring. Therefore, it is of great importance in breeding programmes to predict gain expected from selection for a character (Fehr, 1987; Falconer & Mackay, 1996).

McKendry *et al*. (1988) concluded that all the NUE characteristics studied in their research were under genetic control, with additive gene action being significant for the characteristics thousand kernel mass, hectolitre mass and grain protein. Dominant gene action was detected for certain characteristics but the degree and direction was both trait and genotype specific. The studied characteristics were grain protein concentration, grain protein yield, total N at maturity, N harvest index, grain yield and harvest index. Variance analysis indicated a large genetic component of the variation relative to the environmental component for all the characteristics studied.

Heritability is a not a constant value, as decisions made by the breeder can influence the magnitude of the value and the amount of genetic improvement obtained from selection. Heritability estimates provide an indication of the expected response to selection in segregating populations, and in theory, both h^2_b and h^2_n can vary from 0 to 1. High estimates indicate how well evaluation of the parents will predict what the progenies will be like with a particular combination of breeding material and technique of evaluation (Jones, 1986). Characteristics with high h^2_n values can be improved more rapidly with less intensive evaluation than those with low values and hence h^2_n is useful in calculating selection progress estimates. The h^2_b overestimates the response to selection as it includes non-additive effects (Dudley & Moll, 1969).

2.6.3 Relationship between NUE and other agronomic characteristics

According to Paccaud *et al*. (1985) significant positive correlations for total N at maturity with grain yield (r = 0.68) and harvest index (r = 0.50) was calculated. Significant correlations for total N at maturity with grain protein (r = 0.56), grain yield (r = -0.40), harvest index (r = 0.15) and biological yield (r = 0.92) was found by Day *et al*. (1985). These authors also found positive correlations for NHI and grain protein yield (r = 0.15). McMullan *et al*. (1988) found positive correlations for grain yield and NHI.

The greatest genetic gain due to selection on a yearly basis is usually the goal of the plant breeders. There are various ways to maximise this in breeding programmes. Gain due to selection is defined as:

$\Delta G = i\, \partial_p h^2 = i\, \partial^2_A / \partial_P$

with ΔG defined as the genetic gain due to selection, i defined as the selection intensity, ∂_p defined as the phenotypic standard deviation, h^2 defined as the narrow sense heritability, and ∂^2_A defined as the additive genetic variance. Maximizing any one of these factors, i, ∂^2_A or h^2, will result in a higher genetic gain because of selection

(Henning & Townsend, 2005). Because h^2 is equivalent to $\partial^2_A/ \partial^2_P$ it follows that maximising ∂^2_A relative to ∂^2_P will increase gain because of selection. This typically done by some means of progeny testing to minimize environmental influences, and by choice of parents with high GCA for specific traits on the basis of progeny testing.

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CHAPTER 3

GRAIN YIELD, NITROGEN UPTAKE AND USE EFFICIENCY COMPONENTS OF SOUTH AFRICAN IRRIGATION WHEAT CULTIVARS WITH DIFFERENT NITROGEN MANAGEMENT STRATEGIES

3.1 Introduction

Worldwide interest to increase grain protein percentage of wheat has focused research on nitrogen use efficiency (NUE) of the crop without sacrificing any yield potential (Desai & Bhatia, 1978). This requires that the efficiency of N absorption from either soil or fertilizer (uptake efficiency) and the partitioning of the absorbed N between biomass and grain (utilization efficiency) must be improved (Wuest & Cassman, 1992). In achieving this it is of great importance to ensure an N management strategy, that satisfies the N requirement of a cultivar optimally (Ladha *et al*., 2005).

Nitrogen and water have been shown to exhibit strong synergistic interactions with respect to crop yields, yield components, water use efficiency (WUE) and NUE (Aulakh & Malhi, 2005). They concluded that for achieving maximum NUE and WUE, applications of water and N fertilizer should be optimized in combination to minimize NO_3^- losses from the soil and to maximize N uptake by the crop. These authors also reported that several other factors and processes are of importance in achieving this. Some of them are addressed in the next paragraphs with the emphasis on wheat production.

Usually, uptake and utilization efficiency of N in wheat production varies considerably (Ladha *et al*., 2005). They attributed this phenomenon to the fact that both kinds of efficiency are dependent on various processes like supply, absorption, translocation, assimilation and redistribution in the soil-crop system (Moll *et al*., 1982; Van Sanford & MacKown, 1986). The relative contribution of these processes to genotypic differences in NUE is largely unknown and varies not only among genetic populations but also among fertility environments. Moll *et al*. (1982) observed that at low N supply, differences among genotypes for NUE were largely due to variation in utilization efficiency, but with high N supply, differences were largely due to variation in uptake efficiency. The authors concluded that variation of NUE appeared to result from differences among genotypes and applied levels of N.

Ortiz-Monasterio *et al*. (1997) reported from their studies that the genetic gains with cultivars released over a long period of time in NUE under fertilized conditions are a combination of grain yield potential and lodging resistance. However, when comparing genetic gains in NUE under conditions of no fertilizer applied versus fertilizer applied without the effect of lodging there were no differences between cultivars in their rate of genetic progress. Thus, the semi dwarf cultivars out yielded the previously released tall cultivars with or without the application of N fertilizer, regardless if lodging occurred or not. These authors also showed that there was an improvement in genetic gains concerning NUE between the early and the more recently released semi-dwarf cultivars under conditions of both low and high N fertility.

This result supports the hypothesis that selecting cultivars for NUE under medium to high fertility environments results in germplasm with improved performance under both high and low fertility conditions. They hypothesized that with surplus soil mineral N, uptake efficiency is not limiting. Subsequently, utilization efficiency becomes more important. Since the levels of soil mineral N affect the relative importance of uptake efficiency and utilization efficiency, it seems that the genotype can perceive which component is more limiting under different levels of N supply and in turn adapt to those soil conditions. This flexibility or compensation of genotypes between uptake and utilization efficiencies has possibly contributed to their wide adaptation to diverse fertility environments.

Wuest & Cassman (1992) found that the recovery of N applied at planting ranged from 30 to 55%, while recovery of N applied at anthesis ranged from 55 to 80% in irrigated wheat. Fertilizer N applied at anthesis had the greatest influence on post-anthesis N uptake, which ranged from 17 to 77 kg N/ha. This shows that wheat plants can efficiently utilize late N applications. Applications of post-emergence N have been successfully implemented on irrigated wheat to manipulate yields and the grain protein percentage thereof (Karamanos *et al*., 2005; Ma *et al*., 2006). In this study the grain protein was also influenced by the availability of N in the soil, and its interaction with soil water and temperature. These authors concluded that in contrast to yield, both N applied at seeding and post-emergence influenced grain protein. The impact of N applied at seeding was greater when soil organic matter levels were below 5%. They also confirmed that grain protein does recover once the maximum yield potential of a cultivar under specific agroecological conditions have been reached. Grain protein levels may also increase with late season N applications (Wuest & Cassman, 1992; Ma *et al*., 2006).

Fageria & Baligar (2003) and Ladha *et al*. (2005) reported decreased NUE values with increased N applications with some exceptions in physiological efficiency. Ehdaie *et al*. (2001) found that higher N availability increased biomass (29%), grain yield (16%) and grain protein (5%), but decreased harvest index by 10%, NUE of yield by 28%, N uptake efficiency by 18%, N production efficiency by 12% and N partitioning efficiency by 8%.

Ladha *et al*. (2005) listed three groups of factors controlling fertilizer N loss and subsequently NUE values: (1) factors controlling crop demand for N, (2) factors controlling N losses from soil-plant systems, (3) factors controlling supplies of plant available N from soil and fertilizer. These sets of factors are composed of sub factors, which have a direct or indirect effect on N fertilizer demand, supply and loss. The NUE of a crop can be improved by adopting fertilizer, soil, water and crop management practices that will maximize crop N uptake, minimize N losses, and optimize indigenous N supply. Development of cultivars with higher NUE is also essential, since they will result in lower N requirements. As a general trend, grain yields increase with an increase in total N uptake and some genotypes produce different yields with the same amount of N uptake, indicating differences in the efficiency of N absorption and assimilation, physiological characteristics and efficiency of internal N utilization to produce biomass and grain (Ladha *et al*., 2005).

The high yielding dwarf and semi-dwarf wheat genotypes released during and after the Green Revolution were selected to respond to high N inputs. In the process, genetic selection was aimed for a high harvest index (HI) under medium rates of N fertilization. However, HI and nitrogen harvest index (NHI) respond differently to high levels of N input (Ehdaie *et al*., 2001). Cassman *et al*. (1992) reported that the N supply environment had contrasting effects on HI and NHI in bread wheat. While higher early season N supply increased both biomass and grain yields so that HI was relatively constant or increased slightly, the NHI decreased linearly, indicating reduced utilization efficiency. Furthermore, high N fertilizer input can mask efficiency differences among genotypes in accumulating and utilizing N to produce grain. Ortiz-Monasterio *et al*. (1997) reported that as N supply increased the relative importance of N uptake efficiency decreased and that of N utilization efficiency increased in a diverse set of bread wheat genotypes.

Calculation of NUE is typically based on the amount of N in the crop at maturity. It is commonly perceived that maximum accumulation of N in plants occurs at maturity; however, it is more typical for cereal crops that maximum N accumulation is reached between anthesis and maturity. Dhugga & Waines (1989) found differences among wheat genotypes for biomass N accumulation before and after anthesis at the highest soil N level. At this level, some genotypes either stopped accumulating or showed a net loss of biomass N between anthesis and maturity, which appeared to be associated with superior pre-anthesis N accumulation capacity and reduced grain N yield of such genotypes.

High N fertility levels often increase leaf area indices, but the greatest difference up to maturation is the ability to maintain a larger number of green leaves late in the season as compared with low N fertility levels. Remobilization of vegetative N during grain filling in wheat contributes significantly to final grain N content. Van Sanford & MacKown (1987), working with soft red winter wheat, detected significant cultivar differences in N remobilization from the flag leaf, peduncle, and lower culm to the developing grain. The proportion of N accumulated by the ear ranged among cultivars from 51 to 91%. They also found 83% of the total above ground N at maturity to be already present in the plant at anthesis. An analysis of cultivar differences indicated that all of the cultivar variation in final ear N could be associated with variation in total N uptake. Higher post-anthesis N uptake was associated with lower N utilization efficiency, higher grain N concentration, and lower grain yields (Van Sanford & MacKown, 1987).

Increased fertilizer N generally decreased N uptake and utilization efficiency, despite of an increased grain protein content (Daigger *et al.*, 1976). This phenomenon suggests N losses from the plant and most of it occurred prior to and early in the grain filling period when N is rapidly translocated from other plant parts to the ear. During anthesis, protein in tillers and leaves is degraded to its constituent amino acids and/or NH_3. This indirectly suggests that cultivars with a high HI will have a low plant N loss. Avoiding excess N application could reduce N losses and increase NUE in winter wheat cultivars, and estimates of plant N loss from anthesis to 14 days post-anthesis were greater than that from 14 days post-anthesis to maturity (Daigger *et al.*, 1976). Balanced use of fertilizers is the key to efficient nutrient use and for maintaining soil productivity. This requires an input of N, P and K in the ratios needed to maintain soil fertility to optimize crop productivity and to minimize N losses (Aulakh & Malhi, 2005). Linked to the selection of an adapted cultivar, the best strategy for sustaining high yields, NUE, and WUE with minimal N losses would be split application of fertilizers in combination with an appropriate irrigation schedule to optimise absorption of N from the deep soil profile by plant roots.

Despite soil fertility research programs that have been successful in establishing fertilizer N optimums for selected wheat cultivars, little work has been done to improve NUE in wheat genetically. Therefore, plant breeders need to develop cultivars that can absorb N more efficiently from the soil and effectively partition this absorbed N to the grain for protein synthesis. Such cultivars could minimize loss of N from the soil and make more economic use of the available N (Dhugga & Waines, 1989; Aulakh & Malhi, 2005).

The major small grain cereal growing areas of South Africa and specifically the Summer Rainfall Region have in recent years experienced varying wheat yields with variable grain protein concentrations. With changes in the marketing system of wheat in South Africa, profitability of wheat production now depends on yield and grain protein content, with N influencing both (Dalal *et al*., 1998).

Results from research trials and experiences from commercial enterprises indicated that South African irrigated wheat cultivars responded differently in grain yield and quality to different N management strategies. This phenomenon could be linked to the specific N requirements of each cultivar at certain plant development stages during the growing season, and are probably associated with timing of N applications. Research by Slafer & Rawson (1994) showed that the stage of plant development is critical in the management of N applications, because different physiological growth parameters are affected at different growth stages of plant development.

Usually, N applications at planting, and early (Zadoks 20) to late tillering (Zadoks 25) increases tiller count and ear size (during the spikelet formation phase), and thereby yield potential (Zadoks *et al*., 1974). An application at stem elongation (Zadoks 30) increases the spikelet count per developed ear, and can also increase the formation of late tillers (Slafer & Rawson, 1994). Application during the flag leaf (Zadoks 39) to flowering stages (Zadoks 61) increases the individual kernel mass and more importantly also grain protein concentration at harvest (Zadoks 92). The higher grain protein stem from an increased pool of available N in the plant for translocation during grain filling and senescence (Slafer & Rawson, 1994).

Hence, it is clear that timing of N application can be critical in attaining high grain yield and high grain protein content. In soils with low fertility, most grain yield responses to N fertilizer are due to an increased kernel number/m^2 (either increased ear number or grains per ear) and increased total biomass production (Anderson & Barclay, 1991). Where soils are low in fertility, yields respond more to early application of N than late application. Contrastingly, on soils with high fertility, application of N can be delayed until the onset of stem elongation or even flag leaf stage to control plant growth, and these late applications usually results in high grain protein while maintaining high grain yields (Zhang *et al*., 2006). The total fertilizer N application at planting is to maximize early yield potential development in accordance with the environmental potential. It could also be expected that with this N application strategy there could be a greater probability of N losses from the soil profile due to leaching, runoff and via other ways. The split application of fertilizer N in wheat production under irrigation also intends to decrease potential and real losses of N from the soil profile, while simultaneously increasing NUE of the crop. This is because of improved synchronizing of N demand by the plant and availability of N via this split applications. Raun & Johnson (1999) stated that N fertilization early in the growing season would maximise biomass production in winter wheat. However, if grain production is the only objective, N fertilization can be delayed until later in the growing season without significantly affecting the grain yield.

This study was conducted to quantify the effect of different N management strategies on the grain yield, N uptake and use efficiency of five wheat cultivars planted commercially at Riet River and Loskop irrigation schemes. The ultimate aim was to find an N management strategy ensuring the highest possible grain yield whereof the grain protein percentage still fulfils the grading requirements. However, the emphasis in this chapter is on the NUE of the five cultivars to establish in this regard any genetic differences between them.

3.2 Material and methods

3.2.1 Localities and soils

The trials were conducted at Riet River (Latitude: 29.0667, Longitude: 24.6166, Altitude: 1140 m) and Loskop (Latitude: 25.1778, Longitude: 29.3868, Altitude: 916 m) irrigation schemes in 2000 and 2001. Based on the long term minimum and maximum daily temperatures shown in Table 3.1, Riet River and Loskop are respectively representative of the cooler and warmer areas in the summer rainfall region where wheat is produced under irrigation. Hence the yield potential is generally higher at Riet River than Loskop.

In 2000 the maximum temperatures at Loskop mimicked the long term average values for the largest part of the growing season, while the minimum temperatures were higher in May, June and September, but marginally lower in July, August, October and November. The minimum temperatures at Loskop in 2001 followed the long term pattern to a large extent with slight deviations in September and November. Maximum temperatures were in the same order with July slightly cooler, and August, September and November being warmer than the long-term average for these months.

Table 3.1 Selected temperature data (℃) of Riet River and Loskop irrigation schemes

Locality	Month	Long term Maximum	Long term Minimum	Maximum 2000	Minimum 2000	Maximum 2001	Minimum 2001
Riet River							
	January	34.0	17.9	29.0	15.3	33.6	15.5
	February	32.1	16.9	32.1	17.9	33.1	16.1
	March	30.0	14.4	29.4	16.9	31.2	15.2
	April	26.1	9.9	23.2	11.4	28.7	15.8
	May	23.0	5.0	22.1	4.8	22.5	6.0
	June	18.9	0.8	21.1	1.8	20.4	3.5
	July	19.0	0.0	19.2	0.3	18.5	0.8
	August	22.0	2.7	24.5	2.2	21.6	1.7
	September	26.4	7.5	24.3	5.5	23.8	6.4
	October	28.0	11.1	29.8	11.1	29.4	12.0
	November	30.4	13.8	29.7	11.9	28.0	14.2
	December	32.7	15.7	32.6	15.7	30.7	15.3
Loskop							
	January	31.0	17.7	28.4	16.9	32.1	19.2
	February	30.8	17.1	28.6	18.2	29.4	17.2
	March	29.6	15.4	28.8	17.4	29.4	15.2
	April	27.6	11.1	25.2	11.1	27.2	11.7
	May	25.2	6.0	26.7	11.1	25.7	5.5
	June	22.3	2.4	21.8	5.5	22.6	2.1
	July	22.4	2.0	21.6	1.2	21.9	1.7
	August	25.1	4.9	25.3	4.3	26.7	5.4
	September	28.3	9.7	27.7	10.1	28.4	8.9
	October	29.5	13.6	29.4	12.8	29.4	13.6
	November	29.6	15.8	29.7	14.9	33.6	19.9
	December	30.4	17.1	30.6	17.4	29.7	16.8

The minimum temperatures at Riet River in 2000 showed marginal deviations from the long term average values in June, September and November. However, in this year maximum temperatures were higher than the average values in June, August and October, but slightly lower in September. Minimum temperatures in 2001 were with the exception of August and September higher than the average values. This year the maximum temperatures were above average in June and October but the rest of the growing season below the average values for those months.

The trials at Riet River were planted on a fine sand Hutton 3100 soil form (Soil Classification Working Group, 1991). At Loskop the trials were planted on a fine loamy sand Kimberley 1100 soil form. Selected physical and chemical analyses of these soils prior to planting in 2000 and 2001 are displayed in Table 3.2. The sampling and analysis procedures follow in a later section. Generally these soils' analyses indicated no serious fertility limitations for wheat and N management strategies.

Table 3.2 Selected properties of the trial soils at Riet River and Loskop irrigation schemes in 2000 and 2001

Soil depth (mm)	Nitrogen (kg N/ha)	pH (KCl)	P	K	Ca	Mg	Na	Clay %
					(mg/kg)			
Riet River 2000								
0-200	15.72	5.1	25	112	345	100	10	7
200-400	13.23	5.2	15	129	419	140	14	9
400-600	14.09	5.3	7	119	500	212	17	9
600-900	46.04	5.5	3	116	511	241	12	10
900-1200	43.52	5.7	2	124	493	254	16	8
Total	132.60							
Loskop 2000								
0-200	46.35	5.6	42	274	647	242	16	14
200-400	46.68	5.5	38	269	664	244	21	12
400-600	40.35	5.5	32	236	675	230	16	15
600-900	37.73	5.0	7	168	671	255	33	18
900-1200	30.72	5.0	5	151	651	241	28	19
Total	201.83							
Riet River 2001								
0-200	20.02	5.1	13	114	333	132	6	6
200-400	29.02	5.2	8	123	411	180	5	7
400-600	35.01	5.4	3	121	524	273	2	9
600-900	15.54	5.6	<1	109	486	288	4	9
900-1200	14.14	5.7	<1	105	448	286	4	9
Total	113.23							
Loskop 2001								
0-200	21.77	5.9	11	330	734	287	13	12
200-400	32.53	5.9	6	225	642	232	27	14
400-600	24.77	5.5	1	170	706	296	21	16
600-900	17.34	5.7	<1	90	717	411	42	18
900-1200	14.54	5.6	<1	107	766	441	47	19
Total	110.95							

3.2.2 Experimental layout and treatments

All trials were planted in a complete randomised block design with treatment combinations comprising of cultivars and N management strategies (hereafter referred to as N treatments) replicated three times. As shown in Table 3.3 commercially available cultivars were selected whereof the relative growth periods range from long (Baviaans) to medium (Olifants and SST 876) to short (Steenbras and SST 822). Hence, in addition to yield potential differences due to growth periods, these cultivars also have different agronomic characteristics related to lodging susceptibility and general plant architecture (Anonymous, 2004).

The N treatments consisted of a zero and a recommended N application whereof the latter treatment was split to induce specific crop growth responses as discussed (Table 3.3). On account of the differences in yield potential between localities, total N applications were 220 and 200 kg N/ha in 2000 and 2001 respectively at Riet River, and 180 kg N/ha at Loskop in both years. The N4 treatment tested in 2000 is based on research by CIMMYT stating that this timing of N application until first node growth stage can result in higher grain quality. However, due to the low yield response with this treatment in 2000 it was subsequently adapted in 2001 by increasing the application of N at planting, as similarly implemented by Sayre (1998) in Mexico.

3.2.3 General agronomic practices

At Riet River the trials in both years were planted directly after harvesting the preceding crop of maize. At Loskop, the trials were planted in 2000 directly after harvesting the preceding cotton crop, and in 2001 about six months after harvesting the preceding wheat crop. A conventional tillage system was followed to prepare the seedbed at all trial sites. This implies the residue of the previous crop was disced, and then mouldboard ploughed, before preparation of a suitable seedbed commenced for planting.

The trials were planted at dates falling within the recommended spectrum of the selected cultivars (Anonymous, 2004). Hence, planting dates were at Riet River on 23 June 2000 and 18 July 2001, and at Loskop on 25 May 2000 and 17 May 2001.

In all instances a plot size of eight rows of five metre length, with a row spacing of 17 cm was used. The seed was planted *ca* 2 cm deep into a dry seedbed with a Wintersteiger Plotman experimental planter calibrated for the desired plot length. Thereafter light irrigations were applied to initiate germination and emergence. Standard seeding densities as recommended in the wheat production guidelines were used for the selected cultivars (Anonymous, 2004). These cultivars were planted at a seeding density of 300 seeds/m^2 based on kernel weight of the specific cultivar. Generally it amounted to a seeding density of between 90 and 130 kg seed/ha.

Table 3.3 Cultivar and nitrogen treatments used for the trials at Riet River and Loskop in 2000 and 2001

		Riet River			**Loskop**		
		Nitrogen application (kg/ha)					
Year	**Nitrogen treatment**	**Planting**	**Stem elongation**	**Flag leaf stage**	**Planting**	**Stem elongation**	**Flag leaf stage**
2000	*N0*	0	0	0	0	0	0
	N1	220	0	0	180	0	0
	N2	100	60	60	100	40	40
	N3	100	90	30	60	90	30
	N4	0	220	0	0	180	0
2001	*N0*	0	0	0	0	0	0
	N1	200	0	0	180	0	0
	N2	120	40	40	100	40	40
	N3	80	80	40	60	80	40
	N4	80	120	0	60	120	0

Cultivars

SST 876 Baviaans Steenbras Olifants SST 822

The relevant fertilization recommendations for wheat production under irrigation as published by the Small Grain Institute were used to ensure sufficient supply of essential nutrients such as phosphorus (P) and potassium (K) (Anonymous, 2004). As a result applications of 30 kg P/ha and 20 kg K/ha were broadcasted preceding final seedbed preparations, together with the relevant treatment N applications. The split applications of N as dictated by the N treatments were applied to the relevant plots at the indicated plant growth stage combined with an irrigation application. Limestone ammonium nitrate (28% N), single super phosphate (10.5% P) and potassium chloride (50% K) were used as fertilizer sources.

Irrigation scheduling during the growing season was managed via relevant crop factors combined with daily evaporation pan measurements obtained from weather stations in the immediate vicinity of the trials. Overhead sprinkler irrigation was used and calculated water deficits were replenished at weekly intervals. The trials were also optimally managed with regards to disease, insect and weed control.

Crop yields were measured during November at Riet River and during October at Loskop. All eight rows of a plot were harvested with a Wintersteiger plot harvester at maturity, yielding a harvest area of 6.8 m^2. Grain samples were air-cleaned to remove any foreign material before determining sample weights and grain hectolitre mass following standard grading procedures and regulations.

3.2.4 Sampling and analysis procedures

At planting duplicate soil samples were collected at every replicate with an auger from the 0-200, 200-400, 400-600, 600-900 and 900-1200 mm soil layers. After sampling the duplicate samples were mixed and placed in paper bags to facilitate air-drying and prevent heat build up. These samples were air-dried (48-72 hours) at a room temperature range of 25-30 °C to suspend the continuous mineralization and nitrification processes in soil. The air-dried samples were crushed, sieved (< 2 mm) and stored in dry, cool conditions until analysis for ammonium and nitrate using a colorimetric flow system method (Keeney & Nelson, 1982; Technicon, 1977, 1978). The ammonium and nitrate analysis values were converted to kg N/ha using a bulk density of 1500 kg/m^3 and then added to obtain the total mineral N (kg N/ha) in every layer. The soil samples were also analysed for pH (1:2.5 KCl), P (Bray 1), K, Ca, Mg, Na (Ammonium acetate) and clay content (Hydrometer method) using standard procedures (The Non-affiliated Soil Analysis Work Committee, 1990).

Above ground biomass samples of each treatment combination were collected at maturity from an area of 0.085 m^2 (one row of 50 cm x 17 cm). All plants within this area were cut at ground level, dried until constant weight (60 °C for 24 hours), weighed and threshed. The grain was separated from the residue, before the residue was milled (< 0.2 mm) and the total N concentration determined with a *Leco*-combustion analyzer (*Leco* FP–2000, Nitrogen/Protein Analyzer; Leco Corporation, St. Joseph, MI). Total N concentration was chosen as the method of plant analysis because of its widespread use and reliable analysis technique (Greenwood, 1978; Verstraeten & Vlassak, 1981). A Near-Infrared Reflectometry (NIR) method calibrated against this *Leco*-Combustion Analyser was used to determine the N concentration of the grain.

3.2.5 Data processing and analysis

The N uptake by grain (Ngrain) and residue (Nstraw) for all plots were calculated using the relevant dry matter yields and N concentrations. These values of Ngrain and Nstraw were used to obtain through summation the N uptake by the total above ground biomass (Ntotal). Then the N harvest index (NHI) was calculated as NHI=Ngrain/Ntotal.

In addition to NHI the N agronomic efficiency (NAE), N recovery efficiency (NRE) and N physiological efficiency (NPE) were also calculated (Craswell & Godwin, 1984; Doyle & Holford, 1993):

NAE = (YF-YC)/*F;*
NRE = (NF-NC)/*F* * 100;
NPE = (YF-YC)/(NF-NC);

where YF and YC are respectively the grain yields at the fertilized and unfertilized plots, NF and NC are respectively the N uptake by the total biomass at the fertilized and unfertilized plots, and F the amount of fertilizer applied (McDonald, 1989).

All datasets per locality and year were analysed individually because of the differences in climatic conditions and cropping histories, which resulted in confounded growth and yield responses. The individual datasets were subjected to analysis of variance using Gen Stat 8 (Genstat 8th edition, 2006, Lawes Agricultural Trust). The pair-wise *t*-test ($P_{0.05}$) was used to compare means when F-probabilities were significantly different.

3.3 Results and discussion

Only the results of grain yield and N uptake by either the grain or total biomass will be presented because these three parameters were used in the calculation of NHI, NAE, NRE and NPE. Hence, the ANOVA F-probabilities for these seven measured and calculated components are given in Table 3.4 to obtain a broad perspective of the treatment effects on them.

It is clear that neither the main effects of cultivar and N treatment nor their interaction were consistent over localities and years concerning the seven components. However, the actual treatment effects on each component follow.

Table 3.4 ANOVA F-probabilities for the measured and calculated components at Riet River and Loskop in 2000 and 2001

Source of variation	Yield[a]	Ngrain[b]	Ntotal[c]	NHI[d]	NAE[e]	NPE[f]	NRE[g]
Riet River 2000							
Cultivar	*	*	ns	**	**	**	ns
N treatments	**	**	**	**	**	**	ns
Cultivar*N	ns	ns	ns	ns	ns	ns	ns
CV%	13.1%	14.6%	15.0%	8.8%	12.9%	16.2%	15.5%
Loskop 2000							
Cultivar	**	**	ns	*	*	ns	*
N treatments	**	**	**	ns	ns	ns	ns
Cultivar*N	ns	ns	ns	ns	ns	ns	ns
CV%	11.5%	13.5%	14.7%	13.1%	35.9%	27.6%	38.9%
Riet River 2001							
Cultivar	**	**	**	ns	*	ns	**
N treatments	**	**	**	ns	ns	ns	ns
Cultivar*N	**	*	ns	ns	ns	ns	ns
CV%	13.3%	15.4%	22.3%	21.1%	18.0%	25.0%	24.7%
Loskop 2001							
Cultivar	ns	ns	**	*	**	**	ns
N treatments	**	**	**	**	ns	*	*
Cultivar*N	*	ns	**	*	ns	ns	*
CV%	10.6%	13.0%	14.2%	12.1%	66.0%	70.4%	28.3%

[a] Grain yield; [b] Nitrogen uptake in grain; [c] Total Nitrogen uptake; [d] Nitrogen harvest index; [e] Nitrogen agronomic efficiency for grain yield; [f] Nitrogen physiological efficiency; [g] Nitrogen recovery efficiency

$P_{<0.001}$ ** $P_{0.001 - 0.05}$ * *Non significant* ns

3.3.1 Grain yield

The mean grain yields obtained due to the different treatment combinations at the two irrigation schemes for the two years are displayed in Table 3.5.

Riet River in 2000: A mean grain yield of 4.382 t/ha was recorded (Table 3.5). However, the grain yield of SST 822 was significantly lower than that of the other four cultivars. Following maize in a double cropping system, the residual mineral N content of 43 kg

N/ha to 600 mm depth in the soil at planting (Table 3.2), and linked to the incorporation of the crop residue and subsequent immobilization of plant available N during decomposition, even lower availability of soil mineral N could be expected during the early part of the growing season. This immobilization effect manifested in extremely low grain yields due to the N0 treatment with a mean of 0.708 t/ha. This scenario may have caused the low grain yield of the short growing season cultivar SST 822. In comparison with the N1, N2 and N3 treatments, the N4 treatment also produced a significantly lower grain yield. Again, this indicated insufficient plant available N during early stages of the growing season as a result of either limited amounts of residual soil mineral N or ineffective fertilizer N applications because N was applied at the stem elongation stage. Hence, the radical increases in grain yields with the N1, N2 and N3 treatments.

Table 3.5 Effect of nitrogen treatments on grain yield (t/ha) of wheat cultivars at Riet River and Loskop in 2000 and 2001

Year		Locality											
		Riet River						Loskop					
	Cultivars	Nitrogen treatments						Nitrogen treatments					
		N0	N1	N2	N3	N4	Mean	N0	N1	N2	N3	N4	Mean
2000	Baviaans	0.839	6.593	6.318	5.604	3.556	**4.582b**	6.123	6.497	6.559	7.633	7.509	**6.864b**
	Olifants	0.631	6.044	6.086	5.865	4.192	**4.564b**	5.473	6.654	7.030	7.049	5.949	**6.431b**
	SST 822	0.661	5.649	5.208	4.790	3.085	**3.879a**	5.093	6.000	5.864	5.750	4.930	**5.527a**
	SST 876	0.717	6.096	5.334	6.111	4.435	**4.539b**	5.251	6.124	7.091	7.091	6.773	**6.466b**
	Steenbras	0.690	5.545	6.066	5.891	3.554	**4.349b**	5.347	5.263	5.924	5.944	6.232	**5.742a**
	Mean	**0.708a**	**5.985c**	**5.802c**	**5.652c**	**3.764b**	**4.382**	**5.457a**	**6.107b**	**6.493bc**	**6.693c**	**6.279bc**	**6.206**
2001	Baviaans	0.927a	6.444c	5.495bc	5.345b	5.158b	**4.674b**	3.778a	5.525c	4.058ab	4.761bc	5.009c	**4.626**
	Olifants	0.962a	5.414b	6.429c	6.032bc	6.122bc	**4.992b**	4.117a	4.794ab	5.850b	4.128ab	4.666ab	**4.711**
	SST 822	0.833a	4.467b	4.004b	3.695b	4.372b	**3.474a**	4.108a	4.903a	4.739a	4.736a	4.097a	**4.517**
	SST 876	1.380a	4.681b	6.091c	6.208c	6.452c	**4.963b**	3.642a	4.824b	4.850b	4.695b	4.904b	**4.583**
	Steenbras	1.923a	5.846b	5.891b	5.473b	5.126b	**4.852b**	3.780a	5.924c	5.140bc	4.518ab	5.341c	**4.941**
	Mean	**1.205a**	**5.370b**	**5.582b**	**5.351b**	**5.446b**	**4.591**	**3.885a**	**5.194c**	**4.927bc**	**4.568b**	**4.804b**	**4.676**

Loskop in 2000: A high mean grain yield of 6.206 t/ha was produced (Table 3.5). This may be partially due to the fairly high amount of 130 kg/ha residual mineral N in the soil to 600 mm depth at planting (Table 3.2). Steenbras and SST 822 had significantly lower grain yields than Baviaans, Olifants and SST 876. In contrast to Riet River, a comparatively high grain yield of 5.457 t/ha was recorded due to the N0 treatment, although still significantly lower than at the other N treatments. The grain yields of treatments N1, N2 and N4, as well as N2, N3 and N4 did not differ significantly. The high grain yield at the N0 treatment can be attributed to the higher level of residual mineral N in the soil at planting. This residual mineral N also resulted that treatment N4, where N was only applied at stem elongation, produced grain yields that did not differ from the N1, N2 and N3 treatments. It seems that the higher N fertility conditions suited the long growing Baviaans, Olifants and SST 876 better than the short growing Steenbras and SST 822.

Riet River in 2001: The mean grain yield was 4.591 t/ha (Table 3.5). As in 2000 the grain yield of SST 822 was significantly lower than that of the other four cultivars. The grain yields of the N treatments did not differ significantly with the exception of N0 that was significantly lower. With regards to the interaction between cultivar and N treatment, Steenbras and SST 822 showed no significant response in grain yield to any of the N1, N2, N3 and N4 treatments. However, Baviaans showed a significant grain yield response to the N1 and N2 treatments, while SST 876 and Olifants responded significantly to the N2, N3 and N4 treatments. It is interesting that the grain yield of the N0 treatment was on average 70% higher than in the previous year, *viz* 1.205 versus 0.708 t/ha. This may be due to a much higher (84 versus 43 kg N/ha) residual mineral N in the soil to 600 mm depth (Table 3.2). The higher residual mineral N most probably was the result of a three weeks later planting date (17 July 2001 versus 23 June 2000) allowing for more complete decomposition of less incorporated maize residue (6 t/ha yield in 2001 versus 9 t/ha yield in 2000).

Loskop in 2001: A mean grain yield of 4.676 t/ha was recorded which was 25% less than in 2000 (Table 3.5). This can probably be ascribed to 40% less residual mineral N in the soil to 600 mm depth at planting despite of a six months fallow period (Table 3.2). The soil was fairly dry during fallow because of no irrigation, which resulted in slow decomposition of the wheat residue and hence release of mineral N. Grain yield was therefore significantly lower at the N0 treatment than other treatments where N was applied. The grain yields of the N1 and N2 treatments did not differ significantly, as did that of the N2, N3 and N4 treatments. In contrast to the previous year mean grain yields of the five cultivars were almost similar. However, Baviaans, Olifants and Steenbras responded significantly to the N1, N2 and N4 treatments with higher yields.

Ortiz-Monasterio *et al*. (1997) stated that N use efficient genotypes can be characterized by their ability to produce high grain yields under both low and high N fertility conditions, and genotypes that are N use inefficient only produce acceptably high grain yields under high N fertility conditions. Following this line of reasoning, without considering significant differences between the cultivars, the cultivars were ranked based on grain yield at the different N treatments (Table 3.6). Ranking of the five cultivars at the two localities over the two years were mostly inconsistent. A conclusion on their N use efficiency is therefore not obvious. However, overall it seems that SST 822 was the least efficient cultivar while Baviaans and Olifants were the most efficient cultivars. The N use efficiency of SST 876 and Steenbras was moderate.

Table 3.6 Effect of nitrogen treatments on ranking of grain yield of wheat cultivars at Riet River and Loskop in 2000 and 2001

Year		Locality											
		Riet River						Loskop					
	Cultivars	Nitrogen treatments						Nitrogen treatments					
		N0	N1	N2	N3	N4	Mean	N0	N1	N2	N3	N4	Mean
2000	Baviaans	1	1	1	4	3	**1**	1	2	3	1	1	**1**
	Olifants	5	3	2	3	2	**2**	2	1	2	3	4	**3**
	SST 822	4	4	5	5	5	**5**	5	4	5	5	5	**5**
	SST 876	2	2	4	1	1	**3**	4	3	1	2	2	**2**
	Steenbras	3	5	3	2	4	**4**	3	5	4	4	3	**4**
2001	Baviaans	4	1	4	4	3	**4**	4	2	5	1	2	**3**
	Olifants	3	3	1	2	2	**1**	1	5	1	5	4	**2**
	SST 822	5	5	5	5	5	**5**	2	3	4	2	5	**5**
	SST 876	2	4	2	1	1	**2**	5	4	3	3	3	**4**
	Steenbras	1	2	3	3	4	**3**	3	1	2	4	1	**1**

3.3.2 Grain nitrogen uptake

The mean values of Ngrain at the different treatment combinations applied for two years on the two irrigation schemes are shown in Table 3.7.

Table 3.7 Effect of nitrogen treatments on grain nitrogen uptake (kg N/ha) of wheat cultivars at Riet River and Loskop in 2000 and 2001

Year		Locality											
		Riet River						Loskop					
	Cultivars	Nitrogen treatments						Nitrogen treatments					
		N0	N1	N2	N3	N4	Mean	N0	N1	N2	N3	N4	Mean
2000	Baviaans	18.4	135.6	117.5	115.0	65.1	90.3b	103.3	146.3	144.5	159.8	170.8	**144.9b**
	Olifants	14.1	131.1	118.9	120.2	85.4	94.0b	94.6	142.9	150.3	158.0	149.7	**139.1b**
	SST 822	13.8	119.2	110.7	94.7	62.9	80.3a	95.8	130.8	137.3	135.8	117.1	**123.4a**
	SST 876	13.8	117.1	106.3	108.5	85.3	86.2ab	91.8	138.0	156.9	158.9	149.0	**138.9b**
	Steenbras	14.6	111.9	133.7	122.6	79.0	92.4b	93.3	116.6	136.2	132.2	136.1	**122.9a**
	Mean	**14.9a**	**123d**	**117.4cd**	**112.2c**	**75.5b**	**88.6**	**95.8a**	**134.9b**	**145.0c**	**148.9c**	**144.5c**	**133.8**
	Baviaans	19.2a	141.7b	129.2b	127.6b	119.9b	107.5b	62.9	122.1	103.7	109.8	121.2	**103.9**
2001	Olifants	20.1a	115.3b	152.0c	149.2c	146.2c	116.6b	72.3	124.5	145.2	105.6	119.5	**113.4**
	SST 822	18.6a	97.7b	103.7b	97.6b	110.7b	85.7a	74.1	118.2	116.4	118.4	99.7	**105.4**
	SST 876	25.3a	92.2b	142.0c	152.8c	146.3c	111.7b	59.9	111.0	113.6	107.9	113.6	**101.2**
	Steenbras	41.2a	126.6b	130.9b	121.1b	119.0b	107.8b	59.4	127.9	113.8	101.6	117.9	**104.1**
	Mean	**24.9a**	**114.7b**	**131.6c**	**129.7c**	**128.4c**	**105.9**	**65.7a**	**120.7c**	**118.5bc**	**108.7b**	**114.4bc**	**105.6**

Riet River in 2000: A mean Ngrain of 88.6 kg N/ha was calculated for this trial. SST 822 had the lowest Ngrain, followed by SST 876 that did not differ from the other three cultivars. The N0 treatment predictably had the lowest Ngrain, followed by N4 that was also lower than N1, N2 and N3. The treatments N1 and N2 showed the significantly best responses in Ngrain, followed by N3. The low residual mineral N in the soil at planting can account for the low Ngrain at the N0 and N4 treatments, with the low Ngrain of SST 822, partly due to its low yields.

Loskop in 2000: The mean Ngrain for this trial was 133.8 kg N/ha that was 51% higher than at Riet River in the same year. This coincides with the yield differences reported earlier. Steenbras and SST 822 had the lowest Ngrain, with the other three cultivars not significantly different. The N0 treatment again had the lowest Ngrain, followed by N1 and then N2, N3 and N4 that were not significantly different.

Riet River in 2001: In this trial, the mean Ngrain was 105.9 kg N/ha which is 20% higher than in the previous year. Conditions seem to be better for uptake and translocation of N since grain yield difference was only 5%. The lowest Ngrain was calculated for SST 822, with the other four cultivars not differing significantly. As expected, the N0 treatment had the lowest Ngrain followed by N1, and then the N2, N3 and N4 treatments. The interaction effect indicated that all five cultivars responded significantly to N1, N2, N3 and N4 treatments in comparison with the N0 treatment. However, in comparison with N1, only the Ngrain values of Olifants and SST 822 were higher at the N2, N3 and N4 treatments.

Loskop in 2001: The mean Ngrain for this trial was almost similar as for the previous trial at this locality. There was no significant difference in the Ngrain value of the five cultivars. The N0 treatment had the lowest Ngrain, with the Ngrain values of N1, N2, N3 and N4 similar.

3.3.3 Total biomass nitrogen uptake

The mean values of Ntotal calculated for all treatment combinations at both localities during the two study years are presented in Table 3.8.

Riet River in 2000: A mean Ntotal of 127.9 kg N/ha was calculated for this trial. The Ntotal of SST 876 was only 116.6 kg N/ha while the Ntotal values of the other four cultivars ranged from 128.5 to 132.6 kg N/ha. The mean Ntotal of 17.8 kg N/ha at the N0 treatment was significantly lower than the Ntotal at the N1, N2, N3 and N4 treatments that varied between 151.7 and 161.8 kg N/ha.

Table 3.8 Effect of nitrogen treatments on biomass nitrogen uptake (kg N/ha) of wheat cultivars at Riet River and Loskop in 2000 and 2001

Year	Cultivars	Locality											
		Riet River						Loskop					
		Nitrogen treatments						Nitrogen treatments					
		N0	N1	N2	N3	N4	Mean	N0	N1	N2	N3	N4	Mean
2000	Baviaans	20.7	170.6	158.2	160.4	139.5	129.9ab	119.5	192.4	186.3	195.3	247.4	**188.2**
	Olifants	17.5	177.0	146.4	154.8	163.7	131.9b	110.6	188.2	185.3	217.6	227.0	**185.7**
	SST 822	17.9	163.0	147.1	159.9	154.5	128.5ab	136.0	192.1	187.8	192.8	184.0	**178.5**
	SST 876	15.9	140.2	140.9	140.1	145.7	116.6a	128.1	174.9	230.2	213.4	206.1	**190.5**
	Steenbras	17.0	158.0	165.6	151.8	160.7	132.6b	110.9	164.1	189.0	211.7	183.4	**171.8**
	Mean	**17.8a**	**161.8b**	**151.7b**	**155.4b**	**152.8b**	**127.9**	**121.0a**	**182.3b**	**195.7bc**	**206.2c**	**209.6c**	**183.0**
2001	Baviaans	37.9	284.4	238.1	203.7	269.2	206.6bc	77.7a	154.6b	156.3b	170.7bc	204.4c	**152.8a**
	Olifants	44.9	281.8	298.7	289.4	221.5	227.3c	97.2a	179.4b	245.3c	199.7b	197.7b	**183.9b**
	SST 822	49.2	201.2	179.7	215.9	215.1	172.2a	104.4a	205.0b	198.2b	194.2b	210.1b	**182.4b**
	SST 876	39.9	244.7	228.5	297.2	282.7	218.6bc	94.8a	141.3b	203.4d	156.6bc	190.9cd	**157.4a**
	Steenbras	56.1	247.0	237.4	220.4	187.0	189.6ab	83.6a	221.0c	186.5c	141.1b	214.9c	**169.4ab**
	Mean	**45.6a**	**251.8b**	**236.5b**	**245.3b**	**235.1b**	**202.9**	**91.5a**	**180.3bc**	**197.9cd**	**172.4b**	**203.6d**	**169.2**

Loskop in 2000: The mean Ntotal of this trial was 183.0 kg N/ha. There was no significant difference between the mean Ntotal values of the five cultivars. However, the Ntotal values increased significantly from 121.0 kg N/ha at N0 to 209.7 kg N/ha at N5.

Riet River in 2001: In this trial the mean Ntotal of 202.9 kg N/ha was 59% higher than in 2000 at this locality. As mentioned earlier, this is primarily due to better conditions for N uptake and translocation since the yield difference is negligibly small. The Ntotal values of the cultivars ranged from 172.2 kg N/ha with SST 822 to 227.3 kg N/ha with Olifants. In comparison with the Ntotal of the N0 treatment, the Ntotal values of the N1, N2, N3 and N4 treatments were significantly higher.

Loskop in 2001: The mean Ntotal of 169.2 kg N/ha for this trial was slightly lower than for the previous trial at this locality. Both cultivars and N treatments affected Ntotal significantly. All five cultivars responded positively to the N1, N2, N3 and N4 treatments in comparison with the N0 treatment. The highest Ntotal values realized at N1 for Steenbras, N2 for Olifants and SST 876, and N4 for Baviaans and SST 822.

Ortiz-Monasterio *et al*. (1997) reported with applications of 150 to 300 kg N/ha under irrigation Ntotal values of 138 to 178 kg N/ha, with an average of 163 kg N/ha. This is of a similar order as the mean Ntotal values of the four trials in this study.

3.3.4 Nitrogen harvest index (NHI)

The effects of N treatments on the NHI of wheat cultivars planted for two years at two irrigation schemes are displayed in Table 3.9.

Riet River in 2000: The mean NHI value for this trial was 0.72. However, this index differed significantly between cultivars and N treatments. The highest NHI was at the N0 treatment and the lowest NHI at the N4 treatment, namely 0.83 and 0.50 respectively. At the N1, N2 and N3 treatments the NHI values ranged between 0.72 and 0.77. SST 822 was the cultivar with the lowest NHI, *viz* 0.65 while the NHI values of the other cultivars that ranged between 0.72 and 0.76 were significantly higher.

Table 3.9 Effect of nitrogen treatments on the nitrogen harvest index of wheat cultivars at Riet River and Loskop in 2000 and 2001

Year		Locality											
		Riet River						Loskop					
	Cultivars	Nitrogen treatments						Nitrogen treatments					
		N0	N1	N2	N3	N4	Mean	N0	N1	N2	N3	N4	Mean
2000	**Baviaans**	0.89	0.80	0.75	0.72	0.47	0.72b	0.86	0.78	0.78	0.83	0.70	**0.79b**
	Olifants	0.80	0.76	0.81	0.78	0.52	0.73b	0.85	0.74	0.81	0.73	0.68	**0.76b**
	SST 822	0.77	0.74	0.75	0.59	0.41	0.65a	0.70	0.68	0.74	0.70	0.64	**0.69a**
	SST 876	0.87	0.84	0.75	0.77	0.59	0.76b	0.72	0.79	0.68	0.75	0.73	**0.73ab**
	Steenbras	0.85	0.71	0.81	0.76	0.49	0.72b	0.85	0.71	0.72	0.62	0.74	**0.73ab**
	Mean	**0.83d**	**0.77c**	**0.77c**	**0.72b**	**0.50a**	**0.72**	**0.80**	**0.74**	**0.75**	**0.73**	**0.70**	**0.74**
2001	**Baviaans**	0.52	0.51	0.55	0.63	0.45	0.53	0.81b	0.79a	0.66a	0.65a	0.60a	**0.70b**
	Olifants	0.54	0.43	0.53	0.53	0.66	0.54	0.75c	0.70b	0.60ab	0.53a	0.61ab	**0.64a**
	SST 822	0.42	0.50	0.59	0.45	0.52	0.50	0.72c	0.58ab	0.59abc	0.62bc	0.47a	**0.59a**
	SST 876	0.66	0.40	0.63	0.52	0.52	0.54	0.63ab	0.79c	0.57a	0.70b	0.61ab	**0.66b**
	Steenbras	0.80	0.51	0.57	0.55	0.64	0.62	0.71b	0.58ab	0.62ab	0.72b	0.55a	**0.64ab**
	Mean	**0.59**	**0.47**	**0.57**	**0.54**	**0.56**	**0.55**	**0.72d**	**0.69cd**	**0.61ab**	**0.64bc**	**0.57a**	**0.65**

Loskop in 2000: A mean NHI of 0.74 was calculated for this trial. The N treatments had no significant effect on NHI. However, it ranges between 0.70 at the N4 treatment and 0.80 at the N0 treatment. The NHI values of the cultivars differed significantly from 0.69 with SST 822 to 0.79 with Baviaans.

Riet River in 2001: The mean NHI for this trial was only 0.55 which is 24% less than that of the previous trial at this locality. Neither the cultivar nor the N treatments affected NHI significantly.

Loskop in 2001: The mean NHI of 0.65 for this trial was 12% lower than that of the previous trial at this locality. In this trial, the interaction of cultivar and N treatment affected NHI significantly. The lowest NHI for Baviaans, SST 822, SST 876 and Steenbras realized at N4, while that of Olifants at N3. However, the highest NHI for Baviaans, Olifants and SST 876 realised at N0 and that of SST 876 and Steenbras at N1 and N3 respectively.

As could be expected NHI follows to a large extent the trends of Ngrain and Ntotal since it is an indication of the efficiency of N uptake from the soil by the plant and of N translocation in the plant to the grain. It seems from this study that the N treatment had a larger influence on NHI than cultivar. The N0 treatment generally had higher values indicating that cultivars had the capability to utilize and translocate N more efficient when supply of this nutrient from either soil or fertilizer is limiting. Temperature and water availability, in particular during post anthesis and grain filling, can influence the response of a cultivar to residual mineral N in the soil at planting as well as the N added to the soil with fertilizer. Van Rensburg (1996) reported a mean NHI of 0.81 for a South African wheat cultivar grown under optimum irrigation.

3.3.5 Nitrogen physiological efficiency

The NPE values of the wheat cultivars as affected by the N treatments at two irrigation schemes over two years are displayed in Table 3.10.

Table 3.10 Effect of nitrogen treatments on nitrogen physiological efficiency (kg grain/kg N uptake) of wheat cultivars at Riet River and Loskop in 2000 and 2001

Year	Cultivars	Locality									
		Riet River					Loskop				
		N treatments					N treatments				
		N1	N2	N3	N4	Mean	N1	N2	N3	N4	Mean
2000	**Baviaans**	38.78	41.35	34.05	23.33	**34.38bc**	-3.60	6.10	20.70	12.60	**9.00**
	Olifants	36.05	42.39	38.18	24.23	**35.21bc**	10.80	19.90	13.50	3.90	**12.10**
	SST 822	35.09	34.94	29.03	17.66	**29.18a**	8.30	16.50	3.50	-2.70	**6.40**
	SST 876	43.70	36.62	43.53	28.87	**38.18c**	-0.70	18.30	21.80	18.90	**14.60**
	Steenbras	34.68	36.67	36.11	20.04	**31.87ab**	-3.70	7.70	5.80	11.60	**5.30**
	Mean	**37.66b**	**38.39b**	**36.18b**	**22.83a**	**33.76**	**2.20**	**13.70**	**13.10**	**8.90**	**9.50**
2001	**Baviaans**	23.27	22.90	26.81	18.56	**22.88**	23.59	-0.21	11.21	9.78	**11.09ab**
	Olifants	19.42	22.75	22.15	29.34	**23.41**	7.33	11.71	0.38	5.96	**6.34a**
	SST 822	24.09	26.03	17.12	21.94	**22.29**	8.71	6.75	6.97	-0.07	**5.59a**
	SST 876	19.42	25.25	18.91	21.67	**21.31**	24.96	12.73	21.33	10.23	**17.31b**
	Steenbras	21.28	22.36	21.41	23.86	**22.23**	15.68	13.27	11.61	11.68	**13.06b**
	Mean	**21.50**	**23.86**	**21.28**	**23.07**	**22.43**	**16.05b**	**8.85a**	**10.30a**	**7.51a**	**10.68**

Riet River in 2000: The mean NPE value for the trial was 33.76 kg grain/kg N uptake. SST 822 and SST 876 respectively had the lowest and highest NPE values, *viz* 29.18 and 38.18 kg grain/kg N uptake. The NPE at N4 was significantly lower than at the other N treatments whereof the NPE values were similar.

Loskop in 2000: In this trial, the mean NPE was only 9.50 kg grain/kg N uptake. Neither the cultivars nor the N treatments showed significant effects on NPE. However, the NPE values of the cultivars varied from 5.30 kg grain/kg N uptake with Steenbras to 14.60 kg grain/kg N uptake with SST 876. The NPE values of the N treatments ranged between 2.70 kg grain/kg N uptake at N1 to 13.70 kg grain/kg N uptake at N2.

Riet River in 2001: The mean NPE in this trial of 22.43 kg grain/kg N uptake was 34% lower than in the previous trial at this locality. Neither the cultivars nor the N treatments affected the NPE values. There were also no obvious trends in the NPE values.

Loskop in 2001: The mean NPE of 10.68 kg grain/kg N uptake in this trial was similar to that of the previous trial here. SST 822 and SST 876 had respectively the lowest and highest NPE values, *viz* 5.59 and 17.31 kg grain/kg N uptake. The N1 treatment realised the highest NPE with the other N treatments significantly lower.

On average higher NPE values realized at Riet River than at Loskop, mainly because of the higher grain yields measured at the N0 treatment at Loskop. Generally, either SST 822 or Steenbras had the lowest NPE values and SST 876 the highest NPE. Hence, the response of SST 822 and Steenbras to N can be regarded as poor. Van Rensburg (1996) reported a mean NPE of 27 kg grain/kg N uptake for a South African wheat cultivar grown under optimum irrigation.

3.3.6 Nitrogen agronomic efficiency

The effects of N treatments on the NAE values of wheat cultivars planted at two irrigation schemes for two years are shown in Table 3.11.

Riet River in 2000: The mean NAE for this trial was 20.88 kg grain/kg N applied. Mainly because of low grain yield the NAE of SST 822 was significantly the lowest (18.28 kg grain/kg N applied), while the NAE values of the other four cultivars were mostly similar (20.79 to 22.34 kg grain/kg N applied). The NAE values of the N1, N2 and N3 treatments were similar (22.48 to 23.99 kg grain/kg N applied) but significantly higher than that of the N4 treatment (13.89 kg grain/kg N applied) on account of high grain yields.

Loskop in 2000: In this trial, the mean NAE was only 5.20 kg grain/kg N applied. The N treatments did not affect NAE significantly, which was not the case with the cultivars.

Steenbras and SST 876 had respectively the lowest and highest NAE values namely 2.74 and 8.44 kg grain/kg N applied.

Table 3.11 Effect of nitrogen treatments on nitrogen agronomic efficiency for grain yield (kg grain/kg N applied) of wheat cultivars at Riet River and Loskop in 2000 and 2001

Year	Cultivars	Locality									
		Riet River					**Loskop**				
		N treatments					**N treatments**				
		N1	**N2**	**N3**	**N4**	**Mean**	**N1**	**N2**	**N3**	**N4**	**Mean**
2000	**Baviaans**	26.16	24.91	21.66	12.35	**21.27b**	2.08	2.42	8.39	7.70	**5.15ab**
	Olifants	24.61	24.80	23.79	16.19	**22.34b**	6.56	8.65	8.76	2.64	**6.65ab**
	SST 822	22.67	20.67	18.77	11.02	**18.28a**	5.04	4.28	3.65	-0.90	**3.02a**
	SST 876	24.45	20.99	24.52	16.90	**21.71b**	4.85	10.22	10.22	8.46	**8.44b**
	Steenbras	22.07	24.44	23.64	13.02	**20.79b**	-0.47	3.21	3.32	4.92	**2.74a**
	Mean	**23.99b**	**23.16b**	**22.48b**	**13.89a**	**20.88**	**3.61**	**5.76**	**6.87**	**4.56**	**5.20**
2001	**Baviaans**	27.59	22.84	22.09	21.16	**23.42b**	9.71	1.56	5.46	6.84	**5.89bc**
	Olifants	22.26	27.34	25.35	25.80	**25.18b**	3.76	9.63	0.06	3.05	**4.12ab**
	SST 822	18.17	15.86	14.31	17.70	**16.51a**	4.42	3.51	3.49	-0.06	**2.84a**
	SST 876	16.51	23.56	24.14	25.36	**22.39b**	6.57	6.71	5.85	7.01	**6.54bc**
	Steenbras	19.62	19.84	17.75	16.02	**18.30a**	11.91	7.56	4.10	8.67	**8.06c**
	Mean	**20.83**	**21.89**	**20.73**	**21.21**	**21.16**	**7.27**	**5.79**	**3.79**	**5.10**	**5.49**

Riet River in 2001: The mean NAE of 21.16 kg grain/kg N applied was similar to that of the previous trial at this locality. However, in contrast the N treatments did not affect NAE significantly. The NAE values of SST 822 and Steenbras were significantly lower than that of Baviaans, Olifants and SST 876.

Loskop in 2001: In this trial the mean NAE of 5.49 kg grain/kg N applied was similar to the mean of the previous trial at Loskop. The N treatments again had no significant effect on NAE. However, the NAE values ranged from 2.84 kg grain/kg N applied with SST 822 to 8.06 kg grain/kg N applied with Steenbras.

The high amount of residual mineral N in the Loskop soil at planting resulted in relatively high grain yields for the N0 treatment and hence response to applied N at the other treatments was poor, while the reverse situation is valid for Riet River. It seems that the situation at Loskop was somewhat unusual since NAE values of 17.6 kg grain/kg N applied (van Rensburg, 1996) and 20.7 kg grain/kg N applied (Aulakh & Malhi, 2005) were reported for different wheat cultivars under optimum irrigation. In general, SST 822 had the lowest NAE, followed by Steenbras.

Agronomic efficiency for grain yield (NAE) is calculated as the grain yield increase per kg N applied, and can be used to assess the economic profitability of N applications. With the wheat price of R1450 per ton and an N fertilizer price of R6-00/kg N the calculated ratio for economic benefit is 4.14. Values above this ratio indicate that the yield response to applied N was economically profitable. Because the yield of the control treatment (N0) is deducted from the N treatment response, factors affecting the yield of the control (like residual soil mineral N at planting) will influence the calculated values.

3.3.7 Nitrogen recovery efficiency

The mean values of NRE for all treatment combinations at the two irrigation schemes for the two years are given in Table 3.12.

Riet River in 2000: In this trial, the NRE was 62.6%, with neither the cultivars nor the N treatments significantly different. However, the NRE values ranged from 57.2% with SST 876 to 65.7% with Steenbras, and from 60.8% with N2 to 65.4% with N1.

Loskop in 2000: The mean NRE in this trial was only 43.2%. SST 822 had significantly the lowest NRE although not different from SST 876 and Steenbras. Olifants had significantly the highest NRE value although not different from Baviaans and Steenbras. The NRE varied from 33.7% at the N1 treatment to 49.2% at the N4 treatment, but the difference is not significant.

Table 3.12 Effect of nitrogen treatments on nitrogen recovery efficiency (%) of wheat cultivars at Riet River and Loskop in 2000 and 2001

Year	**Cultivars**	**Locality**									
		Riet River					**Loskop**				
		N treatments*					**N treatments**				
		N1	**N2**	**N3**	**N4**	**Mean**	**N1**	**N2**	**N3**	**N4**	**Mean**
2000	**Baviaans**	68.1	62.5	63.5	54.0	**62.0**	38.1	39.4	39.8	70.0	**46.8b**
	Olifants	72.5	58.6	62.4	66.4	**65.0**	39.4	42.7	59.5	62.7	**51.1b**
	SST 822	66.0	58.7	64.6	62.1	**62.8**	33.8	29.4	32.9	29.9	**31.5a**
	SST 876	56.5	56.8	56.5	59.0	**57.2**	25.9	58.1	47.0	44.5	**43.9a**
	Steenbras	64.1	67.5	65.8	65.3	**65.7**	31.3	44.7	56.6	39.0	**42.9ab**
	Mean	**65.4**	**60.8**	**62.5**	**61.4**	**62.6**	**33.7**	**42.9**	**47.2**	**49.2**	**43.2**
2001	**Baviaans**	123.2	100.1	82.9	115.6	**105.5b**	42.7a	43.7a	51.7ab	70.4b	**52.1**
	Olifants	118.5	126.9	122.2	88.3	**114.0b**	45.6a	82.3b	56.9a	55.8a	**60.2**
	SST 822	76.0	65.2	83.3	83.0	**76.9a**	55.9a	52.1a	49.9a	58.7a	**54.2**
	SST 876	102.4	94.3	128.7	121.4	**111.7b**	25.9a	60.3c	34.3ab	53.4bc	**43.5**
	Steenbras	95.5	90.7	82.2	65.5	**83.4a**	76.4b	57.2ab	31.9a	73.0b	**59.6**
	Mean	**103.1**	**95.4**	**99.9**	**94.8**	**98.3**	**49.3ab**	**59.1bc**	**45.0a**	**62.3c**	**53.9**

Riet River in 2001: An unusual high mean NRE of 98.3% realized at this trial. It is due to the extreme Ntotal values reported earlier (Table 3.7). However, the NRE values of

SST 822 and Steenbras were significantly lower than the NRE values of Baviaans, Olifants and SST 876. There was no difference in NRE at the N treatments.

Loskop in 2001: The mean NRE in this trial was 53.9%. Based on the significant interaction between cultivars and N treatments Baviaans had the highest NRE at N4, Olifants and SST 876 at N2, and Steenbras at N1. The NRE value of SST 822 was not affected by any of the N treatments at all.

In Canada, India and United States of America NRE values of respectively 52, 48 and 56% were reported for irrigated wheat, while in the other countries it varied between 50 and 57% (Ladha *et al*., 2005). Van Rensburg (1996) observed a NRE of 64% with a South African wheat cultivar under optimum irrigation. In this study, similar NRE values were obtained, except for the 98% in the Riet River trial in 2001. However, Ehdaie *et al*. (2001) also found very high NRE values in their trials with different wheat cultivars, *viz* 107 to 138%. The short growing cultivars SST 822 and Steenbras had generally lower NRE values than the medium to long growing cultivars Baviaans, Olifants and SST 876.

3.4 Conclusions

Trials were conducted for two consecutive years at Riet River and Loskop irrigation schemes to quantify the effect of different N management strategies on the grain yield, N uptake and use efficiency components of five commercial wheat cultivars. Analyses of variance showed that neither the main effects of cultivar and N treatment nor their interaction had consistent effects on grain yield, Ngrain, Ntotal, NHI, NPE, NAE and NRE over localities and years. However, notable trends emerged from the actual treatment effects that are of great importance for wheat production under irrigation.

Residual mineral N in the soil at planting had a large influence on abovementioned components and cannot be neglected in studies of this nature. In general, the lowest grain yield, Ngrain and Ntotal realized at N0, followed by N4 and then either N1, N2 and N3. Hence, proper N fertilization is essential for a high grain yield whereof the grain protein concentration fulfills the grading requirements. Unfortunately, the results are not conclusive whether all the required N must be applied at planting or split between planting, stem elongation and flag leaf stages. However, it is clear that at least up to 45% of the required N must be applied at planting regardless of the amount of residual mineral N in the soil.

The longer growing Baviaans, Olifants and SST 876 responded in most instances better to N fertilization than the shorter growing Steenbras and SST 822. This applies for grain yield, Ngrain, Ntotal and NHI. Generally, SST 822 or Steenbras had the lowest and SST 876 the highest NPE values. Application of N had limited affects on NAE and NRE. However, the lowest values for these two efficiency components were recorded with SST 822 and Steenbras.

The fact that Baviaans, Olifants and SST 876 showed better NUE than SST 822 and Steenbras may be attributed to higher biomass production owed to a longer growth period, that coincided with greater uptake and accumulation of N. Ehdaie *et al*. (2001) warned that this is not necessarily in all instances since N supply from either soil and fertilizer must be taken into account. Under low N fertility conditions, uptake efficiency is dominant and under high N fertility conditions, utilization is dominant according to Ortiz-Monasterio *et al*. (1997). Hence, several factors must be considered in the selection of wheat cultivars that have better NUE.

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CHAPTER 4

ASSESSMENT OF NITROGEN USE EFFICIENCY COMPONENTS IN SOUTH AFRICAN IRRIGATED SPRING WHEAT GENOTYPES AND THEIR F_2-OFFSPRING

4.1 Introduction

Wheat (*Triticum aestivum* L.) grain yields have increased substantially since the 1950's. About half of this yield improvement has resulted from genetic increases in grain yield and the other half is due to improved production technologies and practices (Frederick & Bauer, 1999). Genetic improvement in wheat yield was the result of selection for improved agronomic characteristics and resistance to biotic and abiotic stresses (Slafer *et al*., 1993). Processes, which have a significant effect on wheat growth and development, include nutrient uptake and metabolism, photosynthesis and respiration, carbon partitioning, leaf senescence, and plant water relations (Frederick & Bauer, 1999). It is generally believed that grain yield in wheat is a function and integration of all these processes, each of which can be altered by the climatic conditions during the growing season and the cultural practices applied to produce the crop.

At the beginning of the century the important contribution of nitrogen (N) nutrition to grain yield became evident and the synthesis of ammonium from atmospheric N made fertilizers available on a large scale. It was found that available wheat varieties were not proficient in exploiting the increased fertility induced by N fertilizer because of their intrinsic susceptibility to lodging in high yielding environments (Borghi, 1999). Breeders were therefore stimulated to develop a new plant ideotype more adapted to high N fertilization levels with subsequent increased lodging risks, which in time lead to the development of high-input semi-dwarf cultivars. However, the efficiency mechanisms of the plant also become important at very low levels of N availability, when yield levels are below the economical threshold. A recent review of N use efficiency (NUE) in cereal production estimated world-wide efficiencies of only 33% for fertilizer N (Johnson & Raun, 2003), and typically values between 30 and 50% was found by Liao *et al*. (2004) for dryland wheat cultivars in Australia. Van Rensburg (1996) reported an N recovery efficiency value of 64% for a South African spring wheat cultivar in a study under irrigation.

Crop requirement of N is directly related to yield potential and is supplied by fertilizer and non-fertilizer N. It is usually observed that after several decades of crop production in a system of conventional tillage, yield without fertilizer N will be relatively low and constant, consistent with the decreased level of organic N in these soils (Johnson & Raun, 2003). Nitrogen application consistently increases N uptake and grain yields (Soon *et al*., 2006). However, the response to fertilizer N application is variable due to environmental conditions, which include the contribution from non-fertilizer sources.

Higher yielding wheat cultivars are generally shorter, earlier maturing and often have more tillers and ears than earlier released cultivars. Harvest index (HI) of mature crops is the ratio of economic product (grain) to the above ground biomass at harvest (Snyder & Carlson, 1984). It is an indication of the partitioning of dry matter between grain and stems and leaves of the plant. The increased yields with modern cultivars are largely attributed to greater distribution of above ground biomass to the grain, i.e. a higher HI. Harvest index is correlated positively with grain yield and negatively with biological yield. The HI and grain growth rate is also higher in newly developed wheat cultivars. There are however, limits to the possible increases in HI and a value of 50-60 has been estimated (Simmons, 1987). Van Rensburg (1996) reported HI values of between 0.43 and 0.56 for a wheat cultivar under different irrigation water management treatments.

It has been shown that the increases in grain yield in wheat from previous breeding efforts were almost exclusively associated with parallel increases in HI (Slafer *et al*., 1999). The yield improvement was associated with a decline in height caused by the introduction of the *Rht* semi-dwarf genes into wheat germplasm (Simmons, 1987). However, plant height has a biological limit with an optimum height range of between 70 and 100 cm. Wheat varieties with high HI values are known to have higher NUE's (Thomason *et al*., 2002). It has also been reported that wheat varieties that accumulate large amounts of N early in the growing season do not necessarily have high NUE's. Plants must translocate this accumulated N to the grain and must assimilate additional N after anthesis to produce high NUE's (Cox *et al*., 1985). Since most genotypic selection is done under high N fertility conditions, efficiency of N use is often considered second in importance to grain yield. This approach will have to change in response to the worldwide need for increasingly nutrient efficient crops (Thomason *et al*., 2002).

Under field conditions, N in the grain is derived mainly from organic N present as components of vegetative plant parts that is remobilized during grain filling. Leaves may contribute 40%, non-grain spike tissues 23%, the stem 23%, and the roots 16% of the N moving to the grain during mid-grain filling (Simmons, 1987). Lea & Azevedo (2006) reviewed results for the uptake of N from the soil, and concluded that many plant species (barley included) can modify their root architecture to enable them to forage for heterogeneously distributed nutrients in the soil, and that this foraging response normally involves increased proliferation of lateral roots within nutrient-rich soil patches. The authors however noted that although nitrate can stimulate lateral root development, high concentrations of nitrate could also inhibit lateral root development.

The extent of N remobilization in wheat has been expressed by means of the Nitrogen harvest index (NHI), which is defined as the proportion of total aboveground plant N present in the grain. The concentration of N remaining in a vegetative plant part at maturity may also be a good indicator of how extensively N is mobilized from that plant part (Simmons, 1987). Dry matter accumulation, synthesis, translocation, partitioning and accumulation of the photosynthetic products within the plant are controlled genetically, and can be significantly influenced by the environment (Snyder & Carlson, 1984).

Growing environmental concerns and lower commodity prices tend to favor agricultural systems with lower input levels. Studies on genetic gain have shown that, though genetic progress exists at all input levels, genetic gain is lower under low input levels (Ortiz-Monasterio *et al*., 1997; Brancourt-Hulmel *et al*., 2005). This situation may have resulted from breeding that has been conducted under either high or low input fertilizer N treatments. Genetic gain measured under low-input treatments was then probably due to indirect selection. The relative gain of indirect versus direct selection, considering equal selection intensities, depends on heritabilities at both input treatments and genetic correlation between input treatments (Falconer, 1974; 1981). Selection in stress environments will favor selection of adaptation characteristics, while breeding in favorable environments may enhance characters linked to maximum yield potential (Brancourt-Hulmel *et al*., 2005).

Genetic selection is often conducted with high fertilizer inputs to eliminate available N as a variable; however, this can mask efficiency differences among genotypes in accumulating and utilizing N to produce grain (Kamprath *et al*., 1982). Total N taken up was more efficiently utilized in grain yield formation in modern cultivars than older ones, although grain protein concentrations were lower in these grains, modern cultivars also exhibited and enhanced ability to redistribute N into the grains resulting in a higher NHI, and also formed more grain dry matter per grain N unit (Górny *et al*., 2006). This is also consistent with findings that high yielding varieties released during the Green Revolution were selected to respond to high N inputs (Earl & Ausubel, 1983). Consequently, continued efforts are needed to include plant selection under low N, something not often considered a priority by plant breeders, and uncharacteristic of agricultural experiment stations (Raun & Johnson, 1999). Genotypic differences in N uptake have been shown in wheat, and recent studies indicate that plant N uptake is likely to be determined by both the plant growth rate and N availability (Liao *et al*., 2004).

Plant genetic variability can be defined as the heritable character of a particular crop species that shows differences in growth or production in comparison with other cultivars of the same species, under favorable or unfavorable growth conditions (Fageria & Baligar, 2003). The traditional objectives of the wheat breeder are to develop cultivars with a stable, high yield and good grain quality characteristics. For the effective improvement of quality and yields, a plant breeder must have knowledge of the inheritance of quality traits and the joint inheritance of quality and agronomic characteristics (Baker *et al*., 1971).

Delgado *et al*. (2001) stated that several alternatives could be used to improve NUE for specific cropping systems depending on geographical areas, crop rotations and varieties. Split application of N fertilizer when possible and management of the crop rotation system are important to increase NUE. Scavenger crops and deeper-rooted small grains can contribute to improving NUE of the rotation by utilizing N leached below the root zone of the shallow rooted crops. Computer models and new tools that can assess the N status of the aboveground canopy, such as chlorophyll levels, sap NO_3^- concentrations and N indices, combined with other new technology such as precision farming and remote sensing will contribute to improvement in nutrient management.

The use of more N efficient cultivars can either reduce N applications or reduce the environmental risk related to high N use in agriculture. It is therefore evident that studies aimed at improving NUE and related crop responses should assess grain yield. The efficient use of N in the soil-plant system can also result in cultivars producing high yields with high grain protein. There is limited information available on the N-use efficiency components of wheat cultivars currently cultivated under irrigation. The objective of this study was to determine the genetic variability for NUE in selected South African spring wheat cultivars and their F_2-offspring.

4.2 Material and Methods

4.2.1 Parental cultivars

The following seven commercially available spring wheat cultivars were included in this study: Kariega, Marico, Olifants, Steenbras, SST 806, SST 822 and Inia. These cultivars were randomly chosen from the irrigation wheats grown in South Africa. Agronomic characteristics of these cultivars are as follows:

Kariega – High yielding cultivar with good grain quality characteristics and wide adaptability.
Marico – Medium to high yielding cultivar.
Olifants – High yielding cultivar with good grain quality characteristics, and is widely adapted.
Steenbras – Low to medium yielding cultivar, suitable for later planting dates.
SST 806 – High yielding cultivar with reduced lodging susceptibility.
SST 822 – Medium yielding cultivar with double dwarf genes, and is adapted to later planting dates.
Inia – Low to medium yielding cultivar that is adapted to a range of planting dates.

4.2.2 Development of F_2-hybrids

The selected parental cultivars were planted in pots in the greenhouse at the Small Grain Institute near Bethlehem from May to June 2002. It was planted at two-weekly intervals to synchronize pollen availability for cross-fertilization. Applicable fertilization, disease and insect control practices were followed to ensure optimal growth and development of plants. The parents were crossed in a half diallel according to Griffings' method 2, model 1 (Griffing, 1956). A half-diallel design was used because reciprocal differences are not significant in wheat (Joshi *et al*., 2004). The methodology for the crossing of self fertilized crops according to Allen (1980) was used to generate 21 F_1-hybrid combinations. The F_1-hybrid seeds were harvested separately and multiplied in the greenhouse during 2003. The experimental material tested in the field study thus consisted of seven parental cultivars and 21 F_2-offspring (crosses) and is shown in Table 4.1.

4.2.3 Environments

Two irrigated environments were selected to test the experimental material namely Vaalharts and Bethlehem. Vaalharts Research Station is situated in the Northern Cape Province (Latitude: -27.916; Longitude: 24.8333, Altitude: 1153 m above sea level) and represents a warmer irrigation region. Bethlehem is located in the cooler Eastern Highveld region of the Free State Province (Latitude: -28.1626; Longitude: 28.2953; Altitude: 1631 m above sea level).

Table 4.1 Seven parental cultivars and their F_2-offspring tested in field trials at Bethlehem and Vaalharts during 2004

Entry	Parents	F_2-offspring
1.	**Kariega**	
2.	Marico	
3.	Olifants	
4.	Steenbras	
5.	SST 806	
6.	SST 822	
7.	Inia	
8.		Kariega x Marico
9.		Kariega x Olifants
10.		Kariega x Steenbras
11.		Kariega x SST 806
12.		Kariega x SST 822
13.		Kariega x Inia
14.		Marico x Olifants
15.		Marico x Steenbras
16.		Marico x SST 806
17.		Marico x SST 822
18.		Marico x Inia
19.		Olifants x Steenbras
20.		Olifants x SST 806
21.		Olifants x SST 822
22.		Olifants x Inia
23.		Steenbras x SST 806
24.		Steenbras x SST 822
25.		Steenbras x Inia
26.		SST 806 x SST 822
27.		SST 806 x Inia
28.		SST 822 x Inia

4.2.3.1 Soil profile descriptions

The soil profile of the Vaalharts trial site was described as a fine sand *Kimberley* 1100 soil form, and at Bethlehem the soil profile was of the fine loamy Avalon 3200 soil form (Soil Classification Workgroup, 1991).

4.2.3.2 Soil sampling, preparation and N analysis

Duplicate soil samples per replicate were collected prior to planting before fertilization and before harvest at each trial site from the following soil layers: 0 - 200, 200 - 400, 400 - 600, 600 - 900 and 900 - 1200 mm. The results from these soil samples indicate the changes in relative levels of plant nutrients between planting and harvest. Soil samples were placed in paper bags to facilitate air-drying. Dry soil samples were crushed and sieved (< 2 mm) in preparation for analyses. The following soil analyses were done: pH

(KCl), P (Bray 1-method), K, Ca, Mg, Na, acid saturation percentage, clay percentage (hydrometer method), nitrate and ammonium concentrations (Technicon, 1977; 1978; Stevenson, 1982; The Non-affiliated Soil Analysis Work Committee, 1990). Nitrogen analysis values were converted to kg N/ha using a soil density of 1500 kg/m^3 and the nitrate and ammonium content per measured soil layer added and is presented as total mineral N (kg N/ha).

4.3 Experimental layout and treatments

A randomized split plot design was used with parents and crosses as sub treatments and the N treatments as main plots. Three replicates of each treatment were planted.

4.3.1 Nitrogen treatments

Two N treatments were needed to calculate the respective NUE components:

- **Low Nitrogen treatment - LN** - an N omission treatment where only phosphorus (50 kg P/ha) and potassium (20 kg K/ha) were applied.
- **High Nitrogen treatment - HN** - an optimally N managed scenario tested that received similar phosphorus and potassium applications and a recommended rate of N (180 kg N/ha) applied during the growing season at planting (120 kg N/ha), and at stem elongation (60 kg N/ha).

4.3.2 Planting of experimental material in 2004

Each experimental plot consisted of six 1.5 m rows with a 17 cm interrow spacing. Due to the limited seed availability, the seed of the parents and their respective offspring were space-planted (5 cm interplant spacing within the row). The trial at Bethlehem was planted on 8th of July and Vaalharts on 20th of July respectively. The preceding crop planted at Vaalharts was maize (2003/4), while at Bethlehem the previous crop was dryland wheat (2003) in a monoculture cropping system. Conventional soil cultivation practices were followed after harvest and during the fallow period succeeding the previous crop, which included discing, ploughing and seedbed preparation. Border plots were planted between the N treatments and around the trials to limit external environmental effects.

4.3.3 Fertilization

Phosphorus and potassium applications were based on the soil analysis values of the trial sites before planting in 2004. The fertilizer requirement (50 kg P/ha and 20 kg K/ha) was broadcasted and incorporated during final seedbed preparation before the planting of both the respective trials. The N treatment application (120 kg N/ha) was applied to the specified treatment plots at planting and at stem elongation (60 kg N/ha), and was not adjusted for residual soil mineral N at planting.

4.3.4 Additional management factors

Light irrigations were applied after planting to initiate germination and aid seedling emergence. Irrigation scheduling from emergence onwards was managed with relevant crop growth factors linked to daily evaporation pan measurements from weather stations in the vicinity of the trial sites, and overhead sprinkler systems were used to replenish the calculated soil water deficit in both trials. Crop growth was monitored during the growing season to eliminate non-treatment nutritional deficiencies, apply weed, disease and insect control when necessary, and to ensure optimal growth.

4.4 Characteristics measured

Measurements and calculated components are based on studies done by Moll *et al.* (1982), Doyle & Holford (1993), Ortiz-Monasterio *et al.* (1997) and Fageria & Baligar (2003).

4.4.1 Agronomical characteristics

4.4.1.1 Biomass at harvest

At maturity, plants were collected from each genotype x N treatment combination. A sampling area of 1.02 m^2 was used in 2004. The collected biomass samples were dried until constant weight and weighed. Biomass was calculated in grams/m^2: (BM - g/m^2). The crop residue (tiller, leaf and chaff remnants) of the treatment combinations were grounded with a Falling Number AB Laboratory mill fitted with a 0.2 mm sieve, and the milled residue samples analyzed via *Leco* combustion for N concentration: (%Nstraw) (Leco FP-2000, Nitrogen/Protein Analyzer; Leco Corporation, St. Joseph, MI).

4.4.1.2 Grain yield

After threshing of the biomass samples, the collected grain was weighed, and the yield per harvest area calculated in ton per hectare: (t/ha).

4.4.1.3 Hectoliter mass

Hectoliter mass values of the respective grain samples were determined with a Dickey John automated apparatus and is expressed as kilogram per hectoliter: (HM - kg/hl).

4.4.1.4 Thousand kernel mass

The mass of thousand kernels of each genotype x N treatment combination was determined and is expressed as TKM (g).

4.4.1.5 Grain protein percentage

The grain protein percentage of the harvested genotypes were determined via Technicon Infra-Alyzer-400 (calculated as %N x 5.7) and corrected to 12% moisture content. The grain protein is expressed as a percentage: (GP - %).

4.5 Calculated components

4.5.1 Harvest index and Nitrogen uptake components

4.5.1.1 Harvest index

Harvest index (HI) was calculated as the ratio between the grain yield and the total above ground biomass at harvest.

4.5.1.2 Nitrogen uptake (grain)

Nitrogen contained in the grain was calculated as grain yield*grain protein/5.7: (Ngrain - kg N/ha).

4.5.1.3 Total Nitrogen uptake

Total N uptake is the sum of Nstraw and Ngrain: (Ntotal - kg N/ha), where N accumulated in the crop residue at harvest (kg N/ha) was calculated as the total biomass – grain yield * %Nstraw.

4.5.1.4 Nitrogen harvest index

The Nitrogen harvest index (NHI) was calculated as the ratio Ngrain/Ntotal at harvest.

4.5.2 Nitrogen use efficiency (NUE) components

4.5.2.1 Nitrogen uptake efficiency

This component was calculated as the total N uptake/crop N supply (fertilizer N + soil mineral N at planting) * 100: (NupE% - %).

4.5.2.2 Nitrogen use efficiency (grain yield)

This component was calculated as the grain yield/crop N supply (fertilizer N + soil mineral N at planting): (NUEYld - kg grain yield/kg N).

4.5.2.3 Nitrogen utilization efficiency (grain yield)

This component was calculated as the grain yield/total N uptake: (NutEYld - kg grain yield/kg N uptake).

4.5.2.4 Agronomic efficiency (grain yield)

This component was calculated as the [Yield (HN) – Yield (LN)]/fertilizer N: (NAEYld – kg grain yield/kg N).

4.5.2.5 Agronomic efficiency (grain protein percentage)

This component was calculated as [Grain protein (HN) – Grain protein (LN)]/fertilizer N: (AEGP - % grain protein/kg N).

4.5.2.6 Physiological efficiency

This component was calculated as [Grain yield (HN) – Grain yield (LN)]/[N uptake (HN) – N uptake (LN)]: (NPE – kg grain yield/kg N uptake).

4.5.2.7 Recovery efficiency

This component was calculated as [N uptake (HN) - N uptake (LN)]/fertilizer N*100: (NRE - %).

4.6 Statistical analyses

The combined dataset that included both environments (Genotypes X Environments x N treatments) for 2004 were analyzed with Gen Stat 8 (Genstats 8th Edition, 2006, Lawes Agricultural Trust) following applicable procedures for analyses of split plot experimental designs. The N treatments were analyzed as main plots, with the genotypes tested as subplots.

Analysis of variance was done for each of the measured characteristics and calculated components. The ANOVA is used to evaluate the response of each genotype for each characteristic within each experiment. The ordinary ANOVA is an additive model and therefore describes only the main effects effectively (Ehdaie *et al*., 1988). The least significant differences (LSD) for each characteristic were calculated with the Student *t* -test at a 95% confidence level. Correlation matrixes were calculated for all the measured and calculated components for the two environments at both N treatments, and the resultant correlation coefficients tested at a 95% probability level.

4.7 Results and discussion

4.7.1 Soil analyses

The soil analyses results of the two environments (Bethlehem and Vaalharts) for 2004 are listed in Table 4.2. The soil analysis results indicated that there were no limiting soil chemical deficiencies at the two environments with regards to the pH, P, K and other cations. The P analysis values decreased with increasing measurement depth; with the 0-200 mm soil layer showing the highest values linked to historic fertilization and soil cultivation practices. The application of additional P fertilization before planting ensured sufficient availability of this nutrient. The soil mineral N content at planting at Vaalharts was the lowest owed in part to the immobilization effect of recently incorporated crop residue on available mineral N, and decreased residual mineral N was left at harvest of the previous crop. The mineral N content at Bethlehem was also marginally reduced because of the wheat on wheat crop rotation.

Table 4.2 Soil analysis results at planting and harvest ($NH_4^+ + NO_3^-$) in 2004 at Bethlehem and Vaalharts

Sampling depth (mm)	pH KCl	P	K	Ca	Mg	Mineral N at planting	Mineral N at harvest	
			….. (mg/kg)…..				LN	HN
Bethlehem								
0-200	4.53	52.8	222	380	104	26.65	14.84	26.25
200-400	5.03	17.6	127	360	140	25.52	12.05	28.97
400-600	5.40	3.3	76	617	206	22.97	8.24	16.35
600-900	5.40	3.5	99	575	350	21.92	17.10	10.58
900-1200	5.23	5.5	120	537	351	21.33	16.07	14.17
Total						**118.39**	**68.30**	**96.32**
Vaalharts								
0-200	6.07	32.5	119	357	132	13.77	19.98	19.41
200-400	6.20	25.9	135	445	148	12.93	11.59	13.56
400-600	6.13	6.7	142	510	185	13.58	11.32	11.93
600-900	6.10	1.1	107	526	230	18.92	10.17	16.49
900-1200	6.07	0.9	107	595	226	19.26	10.65	24.15
Total						**78.46**	**63.71**	**85.54**

LN - Low Nitrogen treatment

HN - High Nitrogen treatment

4.7.2 Climatological data

The monthly mean minimum and maximum temperatures compared to the long-term averages for the two environments are presented in Figures 4.1 and 4.2 respectively.

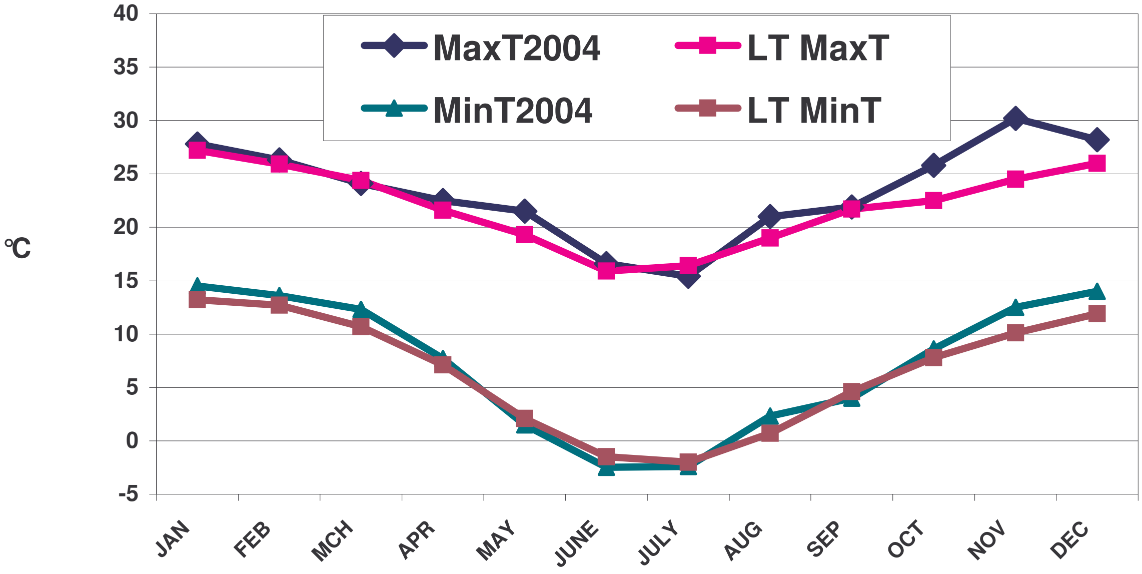

Figure 4.1 **Minimum and maximum temperatures at Bethlehem for 2004**

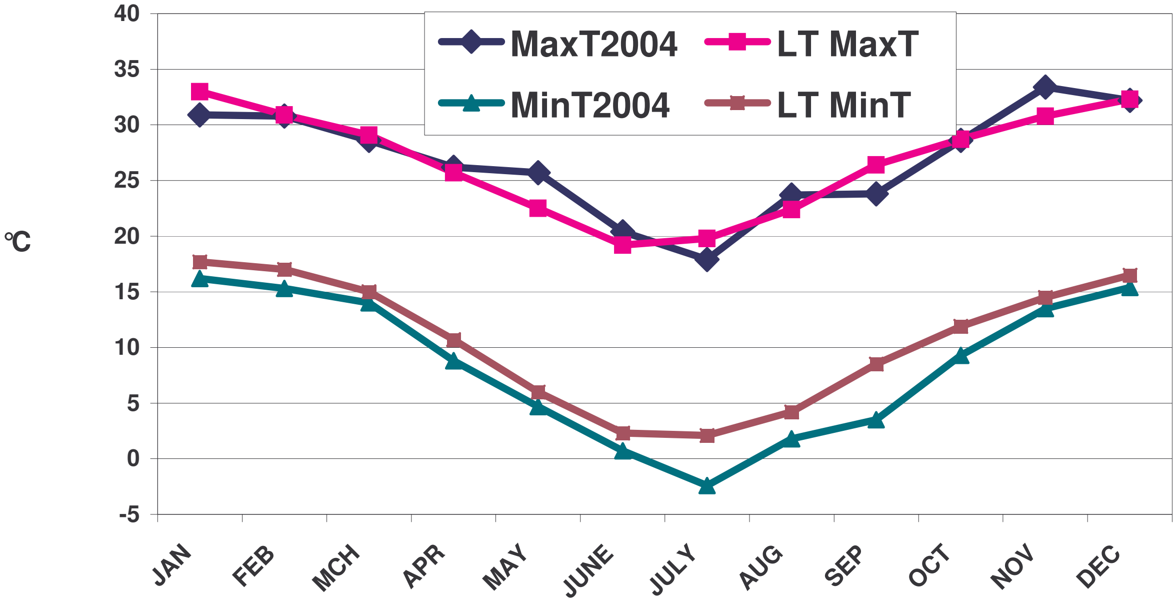

Figure 4.2 **Minimum and maximum temperatures at Vaalharts for 2004**

The mean minimum temperatures at Bethlehem followed the long-term mean values, with the months August to December marginally warmer. The maximum temperatures were above the mean values during the months August to December in 2004. Minimum temperatures at Vaalharts were for most of the cropping season in 2004 below the mean long-term values. Maximum temperatures followed the mean values with deviations in July, August, September and November.

4.7.3 Combined analysis of variance: Agronomic characteristics

The combined ANOVA's for two environments (Bethlehem and Vaalharts) in 2004, for the respective main effects and interactions including the degrees of freedom, mean square errors and related significances for respective agronomic characteristics are presented in Table 4.3.

Biomass

For the measured biomass the main effects of N treatment, Genotype and Environment as well as the interactions between main effects were significant, with the exception of N treatment x Genotype. This indicates that the genotypes responded with increased biomass to N application, although the magnitude of response differed between environments.

Grain yield

Analysis of the grain yield showed the N treatment, Genotype and Environment main effects to be significant. The first order interactions were significant, with the exception of N treatment x Environment. This indicates that the genotypes differed in grain yields measured, and responded differently to applied N. Nitrogen application resulted in a similar response in grain yields at both environments. Genotype responses in yields differed between environments as well as the responses to N applications as indicated by the significant second-order interactions.

Hectoliter mass

The results of the analysis of hectoliter mass (HM) show that N treatment, N treatment x Genotype, and N treatment x Genotype x Environment effects were not significant. This indicates that N applications did not result in a change in measured HM values with the genotypes tested, but that HM values for the respective genotypes differed. The responses to N treatment and with genotypes tested were also changed by interaction with the environment.

Table 4.3 Combined ANOVA for measured agronomic characteristics of wheat genotypes planted at Bethlehem and Vaalharts in 2004

Combined analysis of variance		Mean square values					
Source of variation	**df**	**BM[a]**	**Yld[b]**	**HM[c]**	**TKM[d]**	**GP[e]**	**HI[f]**
Replication	2	94409	0.5196	3.951	1.749	3.1247	0.018405
N treatment	1	24242187**	279.6265**	214.081ns	855.367ns	301.8925**	0.043362ns
Residual	2	7104	0.7848	15.826	58.389	0.4937	0.003702
Genotype	27	98624**	1.4578**	5.921**	40.575**	0.6008**	0.004101ns
N treatment x Genotype	27	40197ns	1.4413**	3.332ns	11.017ns	0.3463*	0.00705**
Residual	108	27524	0.4523	2.426	7.723	0.1846	0.003337
Environment	1	6011600**	417.1306**	665.86**	4956.519**	165.0182**	0.841701**
N treatment x Environment	1	4161532**	0.175ns	27.314**	1.275ns	1.1609ns	0.255367**
Genotype x Environment	27	73766**	1.0696**	6.919**	10.219ns	0.4441ns	0.005132*
N treatment x Genotype x Environment	27	60774**	1.3196**	3.472ns	8.345ns	0.385ns	0.008892**
Residual	112	27812	0.4405	3.009	8.724	0.394	
Total	335						

[a]BM: Biomass; [b]Yld: Grain yield; [c]HM: Hectoliter mass; [d]TKM: Thousand kernel mass; [e]GP: Grain protein percentage; [f]HI: Harvest index.

Thousand Kernel Mass

The Genotype and Environment main effects for thousand kernel mass (TKM) were significant, with N treatment and interactions with Genotype and Environment not significant. Therefore, the genotypes differed in TKM, but N treatment and environment did not change the relative response of these genotypes.

Grain protein

As expected, the N treatment main effect was significant in the ANOVA of grain protein percentage (GP), as well as the main effects of Genotype and Environment. The N treatment x Genotype interaction was also significant, but no significant interaction of N treatment with Environment was evident. This shows the major effect that environment and N treatment can have on GP values, but that genetic variability exists in the response of genotypes to N application.

Harvest Index

The analysis of harvest index (HI) indicated that N treatment x Genotype, Environment and higher-order interactions were significant. Nitrogen applications therefore did not change the mean ratios of grain versus total aboveground biomass values, although biomass was significantly increased. The genotypes also did not differ, which is an indication that the genetic composition with regards to the expression of HI is similar. However, the significant N treatment x Genotype interaction indicates that genetic variation exists in response of genotypes to applied N. The environment also had a significant interaction with N treatment and Genotype, indicating that HI is sensitive to climatic conditions especially during the grain filling period up to physiological maturity. This response is also linked to a similar response observed in TKM and HM.

4.7.4 Combined analysis of variance: Measured Nitrogen uptake and calculated components

The combined ANOVA’s for two environments (Bethlehem and Vaalharts) in 2004, for the respective main effects and interactions including the degrees of freedom, mean square errors and related significances for the respective measured Nitrogen uptake and calculated components are presented in Table 4.4.

Table 4.4 Combined ANOVA for measured and calculated Nitrogen uptake components of wheat genotypes planted at Bethlehem and Vaalharts in 2004

Combined analysis of variance		**Mean square values**		
Source of variation	**df**	**Ngrain**[a]	**Ntotal**[b]	**NHI**[c]
Replication	2	257.3	244.4	0.011
N treatment	1	219894.2**	489890.4**.	0.414545**
Residual	2	691.1	1466.3	0.000519
Genotype	27	734.9**	931.5**	0.006627**
N treatment x Genotype	27	636.3**	618.8*	0.007063**
Residual	108	216.5	341.7	0.002443
Environment	1	263149.5**	312480.6**	0.460132**
N treatment x Environment	1	2679.9**	1.7ns	0.175451**
Genotype x Environment	27	425**	666.6**	0.002772ns
N treatment x Genotype x Environment	27	612**	845.8**	0.005549**
Residual	112	196.5	313.3	0.002163
Total	335			

[a]Ngrain: Nitrogen uptake in the grain; [b]Ntotal: Total Nitrogen uptake; [c]NHI: Nitrogen harvest index.

Nitrogen uptake in the grain and total Nitrogen uptake

The N treatment and Environment main effects resulted in major significant responses in calculated N uptake in the grain (Ngrain), and total N at harvest (Ntotal). The genotypic effect was significant although relatively smaller in magnitude indicating varying responses of the genotypes tested. The interaction of N treatment x Genotype, and Genotype x Environment were significant for the Ngrain and Ntotal values, with the N treatment x Environment showing significant responses in calculated Ngrain values. The second-order interactions were significant for both N accumulation measurements.

Nitrogen harvest index

The calculation and analysis of Nitrogen harvest index (NHI) showed that N treatment, Genotype and Environment main effects were significant, as well as interactions N treatment x Genotype, N treatment x Environment, and N treatment x Genotype x Environment. This indicates that the genotypes differed in N partitioning between the residue and grain, and while the environment affected N application response, genotypes responded similarly in NHI across the two environments. Nitrogen application also resulted in a significant response in calculated NHI values.

4.7.5 Combined analysis of variance: Calculated Nitrogen use efficiency (NUE) components

The combined ANOVA's for two environments (Bethlehem and Vaalharts) in 2004, for the respective main effects and interactions including the degrees of freedom, mean square errors and related significances for the calculated NUE components are presented in Tables 4.5 and 4.6.

Table 4.5 Combined ANOVA for calculated Nitrogen use efficiency components for wheat genotypes planted at Bethlehem and Vaalharts in 2004

Combined analysis of variance		Mean square values		
Source of variation	**df**	**NupE%[a]**	**NUEYld[b]**	**NutEYld[c]**
Replication	2	226.8	28.73	1.35
N treatment	1	29564.4*	13119.68**	7493.04**
Residual	2	504.6	31.6	13.17
Genotype	27	278.1**	49.3**	14.58ns
N treatment x Genotype	27	154.2ns	46.74**	21.04**
Residual	108	115.4	17.89	9.2
Environment	1	45900.7**	5637.05**	65.29*
N treatment x Environment	1	6990.5**	673.16**	491.24**
Genotype x Environment	27	275.7**	51.55**	14.04ns
N treatment x Genotype x Environment	27	330.8**	57.78**	17.61*
Residual	112	109.1	17.72	11.08
Total	335			

[a]NupE%: Nitrogen uptake efficiency; [b]NUEYld; Nitrogen use efficiency for grain yield; [c]NutEYld: Nitrogen utilization efficiency for grain yield.

Table 4.6 Combined ANOVA for calculated Nitrogen use efficiency components for wheat genotypes planted at Bethlehem and Vaalharts in 2004

Combined analysis of variance		Mean square values			
Source of variation	**df**	**AEGP[a]**	**NAEYld[b]**	**NPE[c]**	**NRE[d]**
Replication	2	0.00005428	16.1	29.91	15.9
Environment	1	0.00002484ns	86.49*	47.54ns	718.3*
Genotype	27	0.00002499*	108.63**	334.87**	501.1**
Genotype x Environment	27	0.00002466*	70.6**	256.13**	393.9**
Residual	110	0.00001543	15.99	28.81	126.6
Total	167				

[a]AEGP:Agronomic efficiency for grain protein; [b]AEYld: Agronomic efficiency for grain yield; [c]NPE:Physiological efficiency; [d]NRE: Recovery efficiency.

Nitrogen uptake efficiency

The analysis of calculated N uptake efficiency (NupE%) showed that N treatment, Genotype and Environment effects were significant. The interactions between N treatment and Genotype were not significant indicating that the genotypes responded similarly by increasing plant N accumulation when fertilizer N was applied. The first-order and second-order interactions with the environment were significant.

Nitrogen use efficiency for grain yield

All the main effects and interactions were significant for calculated N use efficiency for grain yield (NUEYld), with N treatment and Environment showing a relatively greater effect. The significant N treatment x Genotype interaction indicated that genotypes responded differently to the two N treatments. This indicates that certain genotypes are more adapted to low N and others at high N scenarios.

Nitrogen utilization efficiency of grain yield

This calculated component measure the efficiency of grain yield responses of the tested genotypes on the basis of N accumulated in the biomass. The analysis of N utilization efficiency of grain yield (NutEYld) indicated that N treatment was significant, directly related to the positive effect of applied N fertilizer on N accumulation (Ntotal) as discussed previously.

The tested genotypes showed non-significance for NutEYld, the Environment main effect was significant, as well as the N treatment x Environment interaction, again pointing to the effect of crop rotation on the N availability aspect combined with N fertilizer application which is the basis of this calculated component. The Genotype x Environment interactions was not significant. This reflects that the responses in NutEYld is a function of the genotypic and N treatment effects, and are not largely influenced by the cropping environment.

Agronomic efficiency for grain protein percentage

The calculation of agronomic efficiency for grain protein percentage (AEGP) showed significant effects for Genotype and Genotype x Environment interactions (Table 4.6). These significant effects indicate that the genotypes not only differed in yield, but also in grain protein response to yield levels and the N availability at the two environments.

Agronomic efficiency for grain yield

The Environment, Genotype and Genotype x Environment interactions were significant for agronomic efficiency for grain yield (NAEYld), in part due to the genetic differences in grain yield.

Physiological efficiency

The calculated physiological efficiency (NPE) showed significant Genotype and Genotype x Environment interaction effects. The main effect of Environment did not have a significant effect on NPE.

Recovery efficiency

The recovery efficiency (NRE) showed significant effects for Environment, Genotype and Genotype x Environment interaction. In all cases, the significant genotype effects indicate variability in response for these components, and different responses across environments.

4.7.6 Tables of means: Bethlehem

4.7.6.1 Measured agronomic characteristics

The results of the measured agronomic characteristics, N uptake measurements and calculated NUE components in 2004 for the Bethlehem environment are listed in Tables 4.7, 4.8 and 4.9.

Biomass

The biomass (BM) values and means for the parents and genotypes measured at harvest are listed in Table 4.7. The mean BM production at harvest was 1164.3 g/m^2. The N treatment main effect differed significantly with HN at a higher value. The parental cultivars Olifants, SST 806 and Steenbras had the highest BM at the LN treatment, while Kariega, Marico and Olifants produced the highest BM at the HN treatment. Olifants and Kariega produced the highest mean BM over the N treatments, with only SST 822 at a significantly lower biomass at both N treatments and on average due to the semi-dwarf ideotype of this cultivar.

The crosses differed significantly in measured BM. The cross with the highest BM of 1267.1 g/m^2 at the LN treatment was Marico x SST 806, followed by Marico x Steenbras, and SST 806 x SST 822. At the HN treatment the cross Marico x SST 806 also had the highest BM (1588.3 g/m^2), followed by Olifants x Steenbras and Kariega x SST 806. The parental cultivars with the highest BM also produced the highest BM in respective crosses.

Grain yield

The mean grain yield was 5.068 t/ha, and the HN treatment significantly increased yields. SST 806 at a grain yield of 4.960 t/ha, followed by Inia at 4.886 t/ha, produced

Table 4.7 Mean agronomic characteristics for seven parental cultivars and their F $_2$-offspring planted at Bethlehem at two N treatments in 2004

Genotypes	BM[a]			Yld[b]			HM[c]			TKM[d]			GP[e]		
	LN	HN	Mean	LN	HN	Mean	LN	HN	Mean	LN	HN	Mean	LN	HN	Mean
Kariega	995.7	1416.7	1206.2	4.375	6.740	5.558	79.10	76.80	77.95	36.53	32.07	34.30	11.09	12.68	11.88
Marico	987.0	1381.3	1184.2	3.667	7.001	5.334	78.90	80.40	79.65	29.47	32.53	31.00	11.38	13.08	12.23
Olifants	1062.2	1372.2	1217.2	4.357	6.297	5.327	76.53	75.03	75.78	27.27	26.40	26.83	11.41	13.92	12.67
Steenbras	1043.4	1194.7	1119.1	3.688	4.943	4.315	79.97	77.20	78.58	33.07	27.20	30.13	12.16	13.83	12.99
SST 806	1047.5	1177.9	1112.7	4.960	5.354	5.157	79.27	76.23	77.75	32.67	28.73	30.70	11.38	12.87	12.13
SST 822	780.6	1014.9	897.7	3.342	4.985	4.163	77.57	77.00	77.28	38.53	30.73	34.63	11.42	13.96	12.69
Inia	1077.3	1154.6	1115.9	4.886	5.574	5.230	78.60	78.27	78.43	35.00	35.07	35.03	11.79	13.49	12.64
Kariega x Marico	1113.7	1319.0	1216.3	4.854	5.168	5.011	77.53	76.23	76.88	31.60	28.60	30.10	10.82	13.54	12.18
Kariega x Olifants	911.4	1501.4	1206.4	3.855	6.381	5.118	77.60	73.97	75.78	33.13	26.53	29.83	11.35	14.05	12.70
Kariega x Steenbras	1183.4	1226.9	1205.2	5.294	5.141	5.218	80.57	76.07	78.32	37.27	27.40	32.33	10.91	13.64	12.28
Kariega x SST 806	707.1	1507.6	1107.3	3.380	6.235	4.807	77.47	75.10	76.28	34.60	28.67	31.63	11.47	13.03	12.25
Kariega x SST 822	850.4	1421.0	1135.7	3.396	6.138	4.767	77.63	78.53	78.08	34.93	32.67	33.80	11.36	13.28	12.32
Kariega x Inia	914.8	1293.1	1104.0	4.092	5.360	4.726	77.87	76.93	77.40	36.60	30.00	33.30	11.70	13.42	12.56
Marico x Olifants	1106.9	1479.2	1293.0	4.961	6.359	5.660	78.67	79.00	78.83	31.60	30.93	31.27	10.96	13.36	12.16
Marico x Steenbras	1222.3	1311.1	1266.7	4.972	4.527	4.749	78.43	78.40	78.42	32.00	29.07	30.53	11.33	13.13	12.23
Marico x SST 806	1267.1	1588.3	1427.7	4.225	7.609	5.917	77.57	79.57	78.57	34.53	30.93	32.73	11.40	12.87	12.14
Marico x SST 822	1038.8	1319.1	1179.0	5.267	5.886	5.577	80.50	75.13	77.82	32.47	26.47	29.47	11.83	14.07	12.95
Marico x Inia	948.5	1170.8	1059.7	3.423	5.893	4.658	76.90	76.53	76.72	28.87	30.73	29.80	12.26	13.57	12.91
Olifants x Steenbras	1166.0	1581.8	1373.9	3.680	6.960	5.320	78.27	78.10	78.18	28.73	30.07	29.40	11.79	14.02	12.90
Olifants x SST 806	858.8	1345.7	1102.3	3.981	6.578	5.279	77.93	76.97	77.45	31.67	28.07	29.87	11.84	13.74	12.79
Olifants x SST 822	1063.2	1116.1	1089.7	4.325	4.944	4.635	78.13	74.37	76.25	31.47	26.53	29.00	11.60	14.51	13.05
Olifants x Inia	1063.1	1324.2	1193.7	4.076	6.339	5.207	78.77	79.20	78.98	32.70	34.60	33.65	11.42	14.36	12.89
Steenbras x SST 806	893.1	1264.4	1078.8	4.133	5.752	4.942	77.73	78.07	77.90	32.80	30.53	31.67	12.19	13.56	12.88
Steenbras x SST 822	974.0	1404.1	1189.1	3.935	7.115	5.525	77.40	78.73	78.07	34.33	32.87	33.60	12.45	13.75	13.10
Steenbras x Inia	920.2	1174.0	1047.1	3.939	5.167	4.553	78.90	78.90	78.90	36.80	32.93	34.87	11.43	13.96	12.70
SST 806 x SST 822	1193.9	1449.7	1321.8	5.327	6.871	6.099	78.23	76.83	77.53	34.80	31.53	33.17	11.71	13.51	12.61
SST 806 x Inia	960.1	1111.1	1035.6	3.053	5.337	4.195	78.13	77.73	77.93	32.93	31.93	32.43	10.95	13.33	12.14
SST 822 x Inia	845.1	1384.6	1114.8	3.551	6.148	4.850	77.43	77.57	77.50	35.73	32.40	34.07	11.98	13.24	12.61
Mean	**1007.0a**	**1321.6b**	**1164.3**	**4.178a**	**5.957b**	**5.068**	**78.271a**	**77.245a**	**77.76**	**33.29a**	**30.22a**	**31.76**	**11.55a**	**13.563b**	**12.56**

[a]BM: Biomass; [b]Yld: Grain yield; [c]HM: Hectoliter mass; [d]TKM: Thousand kernel mass; [e]GP: Grain protein percentage; [f]HI: Harvest index.

LSD (0.05)	281.2	255.2	187.7	1.196	1.427	0.920	2.22	2.76	1.75	4.44	4.76	3.22	0.87	0.82	0.59
LSD (0.05) G x N			268.6			1.402			2.77			5.32			1.00
CV%			14.10%			15.90%			2.00%			8.90%			4.10%

the highest yield at the LN treatment. At the HN treatment Marico produced the highest yield of 7.001 t/ha, followed by Kariega and Olifants. Kariega was the parent with the highest mean yield (5.558 t/ha), followed by Marico and Olifants, with Steenbras and SST 822 significantly lower. The response in grain yield to N application is consistent with reports from literature (Soon *et al*., 2006).

The cross SST 806 x SST 822 had the highest yield at the LN treatment (5.327 t/ha), followed by Kariega x Steenbras and Marico x SST 822. Marico x SST 806 (7.609 t/ha), Steenbras x SST 822, Olifants x Steenbras and SST 806 x SST 822 had the highest yields at the HN treatment. The cross SST 806 x SST 822 had the highest mean yield, followed by Marico x SST 806 and Marico x Olifants. Marico and Kariega showed the highest increases in yields due to the HN treatment, with the crosses Marico x SST 806, Olifants x Steenbras, Steenbras x SST 822 and Kariega x SST 806 showing positive increases. The respective responses at the LN and HN treatments indicate genetic variability of genotypes for grain yield under varying N availability conditions.

Hectoliter mass

The measured hectoliter mass (HM) values showed a mean of 77.76 kg/hl, with the N treatment main effect non-significant. The parental wheat cultivars responded differently to the N treatments for HM. The highest HM at the LN treatment was measured at the parents Steenbras (79.97 kg/hl), SST 806 (79.27 kg/hl) and Kariega (79.10 kg/hl). Marico (80.40 kg/hl) and Inia (78.27 kg/hl) showed the highest HM values at the HN treatment. The highest mean HM was measured with Marico, followed by Steenbras and Inia with Olifants significantly lower.

The crosses Kariega x Steenbras, Marico x SST 822 and Steenbras x Inia had the highest HM at the LN treatment, while Marico x SST 806, Olifants x Inia and Marico x Olifants showed the highest values at the HN treatment. The crosses with the highest mean HM were Olifants x Inia, Steenbras x Inia and Marico x Olifants. The parental cultivars with the highest HM at the respective N treatments also produced the highest HM in their respective crosses.

Thousand kernel mass

The overall mean value for thousand kernel mass (TKM) was 31.76 g, with the N treatment main effect non-significant. The parental cultivars responded differently to the N treatments for TKM. SST 822, Kariega and Inia had the highest TKM values at the LN treatment, with Marico and Inia showing the highest values at the HN treatment. The highest mean values were found for Inia, SST 822 and Kariega with the other parents significantly lower. The crosses Kariega x Steenbras, Steenbras x Inia, Kariega x Inia and SST 822 x Inia had the highest TKM values at the LN treatment. The cross Olifants x Inia had the highest value at the HN treatment, followed by Steenbras x Inia, Steenbras x SST 822, Kariega x SST 822. The parental cultivars with the highest TKM values at both N treatments also showed the highest values in their respective crosses.

Grain protein percentage

The grain protein percentage (GP) results indicate a mean of 12.56% for the Bethlehem environment. The parental cultivars reacted similarly in GP to the two N treatments, with the HN treatment significantly increasing GP from 11.55% to 13.56% on average. The parent Steenbras had the highest GP (12.16%) at the LN treatment followed by Inia and SST 822. SST 822 had the highest GP value (13.96%) at the HN treatment, followed by Olifants and Steenbras. Steenbras was the parent with the highest mean GP, followed by SST 822 (in part due to the lower yields of these two cultivars), Olifants and Inia, with Marico, SST 806 and Kariega at significantly lower values.

At the LN treatment, the cross Kariega x Marico had the lowest GP, followed by Kariega x Steenbras, SST 806 x Inia and Marico x Olifants. Steenbras x SST 822 had the highest GP (12.45%) at the LN treatment followed by Marico x Inia and Steenbras x SST 806. The crosses responded positively at the HN treatment and the highest GP values were found for Olifants x SST 822, Olifants x Inia and Marico x SST 822. Steenbras x SST 822 had the highest mean GP of the crosses, followed by Olifants x SST 822 and Marico x SST 822. Olifants x Inia and Olifants x SST 822 showed high responses to N application, as well as Kariega x Steenbras, Kariega x Marico and Kariega x Olifants. The responses of the genotypes to N application indicate genetic variability for increasing GP at low and high N availability scenarios. The negative correlation between yield and GP was also evident from the results.

Harvest index

Harvest index (HI) is the ratio of the grain yield to the total aboveground biomass at harvest, and is an indication of the partitioning efficiency of the plant. A mean HI of 0.436 was calculated for the wheat genotypes grown at Bethlehem. The N treatment main effect was not significant. This lack of response in HI was also reported by van Ginkel *et al*. (2001) who tested wheat populations under five N selection regimes. The reponses of the genotypes were significantly different. The highest HI at the LN treatment for the parental cultivars was calculated for SST 806 (0.474), followed by Inia and Kariega, with Steenbras and Marico significantly lower. At the HN treatment, the parental cultivar SST 822 had the highest HI of 0.525, followed by Marico, Inia and Kariega, with Steenbras significantly lower. SST 822, Inia and Kariega had the highest HI values on average for the two N treatments.

The cross Marico x SST 822 had the highest HI of 0.523 at the LN treatment, with Kariega x SST 806, Steenbras x SST 806 and Olifants x SST 806 with high HI values. Steenbras x SST 822 had the highest HI value (0.507) at HN, followed by Marico x Inia, Olifants x SST 806, Marico x SST 806 and Olifants x Inia. On average, the crosses Marico x SST 822, Olifants x SST 806 and SST 806 x SST 822 had the highest HI values. The differences in response in HI values of the genotypes indicate that the different N availability levels affected plant growth and biomass development, and partitioning to the grain depended on the genetic combination of the genotype.

4.7.6.2 Measured Nitrogen uptake and calculated components

Nitrogen uptake of the grain

Results for the calculated N uptake of the grain (Ngrain) showed that the HN treatment resulted in significantly higher grain N uptake (Table 4.8). At the LN treatment, Inia had the highest Ngrain value of 100.56 kg N/ha, followed by SST 806 and Olifants, with Marico significantly lower. At the HN treatment, Marico had the highest Ngrain (160.43 kg N/ha) that did not differ significantly from Olifants, Kariega and Inia.

The highest mean Ngrain was calculated for Olifants (119.76 kg N/ha), followed by Kariega, Marico and Inia. SST 822 (94.65 kg N/ha) and Steenbras (99.04 kg N/ha) had significantly lower values. The highest Ngrain values at the LN treatment were calculated at the crosses Marico x SST 822, SST 806 x SST 822 and Kariega x Steenbras. At the HN treatment the crosses Marico x SST 806, Steenbras x SST 822 and Olifants x Steenbras had the highest Ngrain values.

The interaction between Genotype and N treatment indicated that all the genotypes except Marico x Steenbras responded significantly in Ngrain values to the HN treatment, although varying in magnitude. The crosses SST 806 x SST 822, Steenbras x SST 822 and Marico x SST 806 had the highest mean Ngrain values with SST 806 x Inia at a significant lower value. The highest increase in Ngrain at the HN treatment was calculated at the crosses Olifants x Steenbras, Marico, Marico x SST 806 and Steenbras x SST 822. The lowest response to HN was found in the Marico x Steenbras and Kariega x Steenbras crosses.

Table 4.8 Mean Nitrogen uptake and calculated components for seven parental cultivars and their F_2-offspring planted at Bethlehem at two N treatments in 2004

Genotypes	Ngrain[a]			Ntotal[b]			NHI[c]		
	LN	**HN**	**Mean**	**LN**	**HN**	**Mean**	**LN**	**HN**	**Mean**
Kariega	85.29	149.62	117.46	102.59	193.76	148.17	0.834	0.772	0.803
Marico	73.84	160.43	117.14	95.62	199.78	147.70	0.761	0.803	0.782
Olifants	86.92	152.60	119.76	107.22	189.17	148.19	0.809	0.806	0.807
Steenbras	78.57	119.51	99.04	106.40	161.33	133.86	0.739	0.744	0.742
SST 806	99.02	120.77	109.89	115.85	149.98	132.92	0.855	0.806	0.831
SST 822	67.27	122.03	94.65	84.19	155.38	119.78	0.800	0.800	0.800
Inia	100.56	131.75	116.16	122.65	160.82	141.74	0.818	0.817	0.818
Kariega x Marico	92.74	122.46	107.60	115.29	173.57	144.43	0.812	0.707	0.759
Kariega x Olifants	76.75	157.27	117.01	97.07	213.62	155.34	0.795	0.743	0.769
Kariega x Steenbras	101.49	122.54	112.01	122.85	166.47	144.66	0.826	0.735	0.781
Kariega x SST 806	68.11	142.44	105.27	81.75	197.56	139.65	0.840	0.722	0.781
Kariega x SST 822	67.61	144.13	105.87	84.11	188.01	136.06	0.807	0.754	0.781
Kariega x Inia	83.39	125.92	104.66	100.35	169.05	134.70	0.830	0.747	0.789
Marico x Olifants	95.13	148.89	122.01	112.60	192.26	152.43	0.849	0.776	0.813
Marico x Steenbras	98.31	104.17	101.24	121.54	148.39	134.97	0.810	0.698	0.754
Marico x SST 806	85.21	171.74	128.47	114.78	209.01	161.89	0.729	0.823	0.776
Marico x SST 822	109.44	145.22	127.33	126.60	199.16	162.88	0.869	0.734	0.802
Marico x Inia	73.86	140.58	107.22	100.76	172.76	136.76	0.720	0.817	0.769
Olifants x Steenbras	76.14	170.88	123.51	102.99	216.29	159.64	0.731	0.788	0.760
Olifants x SST 806	82.37	158.31	120.34	97.88	192.79	145.34	0.839	0.820	0.830
Olifants x SST 822	88.16	125.80	106.98	112.42	162.48	137.45	0.788	0.775	0.782
Olifants x Inia	81.30	158.64	119.97	102.10	193.26	147.68	0.798	0.820	0.809
Steenbras x SST 806	88.82	137.05	112.94	106.80	174.33	140.56	0.831	0.787	0.809
Steenbras x SST 822	86.20	171.36	128.78	108.31	206.71	157.51	0.790	0.830	0.810
Steenbras x Inia	79.24	125.36	102.30	96.22	163.68	129.95	0.822	0.768	0.795
SST 806 x SST 822	109.36	162.59	135.97	133.19	202.28	167.73	0.822	0.803	0.813
SST 806 x Inia	58.57	124.41	91.49	76.74	150.79	113.76	0.759	0.826	0.793
SST 822 x Inia	74.80	142.76	108.78	92.41	180.91	136.66	0.812	0.788	0.800
Mean	**84.59a**	**141.4b**	**112.99**	**105.05a**	**181.56b**	**143.30**	**0.8034a**	**0.7789b**	**0.791**

[a] Ngrain: Nitrogen uptake in the grain; [b] Ntotal: Total Nitrogen uptake; [c] NHI: Nitrogen harvest index.

LSD (0.05)	24.19	31.25	19.53	28.85	35.90	22.77	0.086	0.071	ns
LSD (0.05) G x N			32.20			41.46			0.077
CV%			15.10%			13.90%			6.10%

Total Nitrogen uptake

The calculated total N uptake at harvest (Ntotal) for the wheat trial had a mean of 143.30 kg N/ha. The HN treatment significantly increased Ntotal from 105.05 kg N/ha to 181.56 kg N/ha. Significant differences were found for Ntotal between the parental cultivars at both the low and high N levels. Inia was the parent with the highest Ntotal at the LN treatment of 122.65 kg N/ha, followed closely by SST 806, Olifants and Steenbras, with SST 822 significantly lower. Marico had the highest value at the HN treatment of 199.78 kg N/ha, but not significantly different from Kariega and Olifants. On average, Olifants had the highest Ntotal of the parents (148.19 kg N/ha) with only SST 822 (119.78 kg N/ha) significantly lower.

The highest Ntotal at the LN treatment was observed for the cross SST 806 x SST 822 (133.19 kg N/ha), followed by Marico x SST 822 and Kariega x Steenbras. At the HN treatment, Olifants x Steenbras (216.29 kg N/ha), Kariega x Olifants, Marico x SST 806 and Steenbras x SST 822 had the highest total N uptake values. The highest responses in Ntotal to the HN treatment were observed in the crosses Kariega x Olifants, Kariega x SST 806 and Olifants x Steenbras.

Nitrogen harvest index

Nitrogen harvest index (NHI) is the calculated ratio between the N taken up in the grain and the total N taken up into the aboveground biomass, and is an indication of the partitioning of N to the grain. The calculated NHI showed that the N treatment significantly reduced the NHI in both the parental cultivars and their F_2-offspring from 0.8034 at LN to 0.7789 at the HN treatment. At the LN treatment, the parent SST 806 had the highest NHI of 0.855, followed by Kariega and Inia, with only Steenbras significantly lower. At the HN treatment, the parents Inia (0.817), SST 806 (0.806) and Olifants (0.806) had the highest NHI values. Averaged over N treatments, SST 806, Inia and Olifants had the highest NHI values.

The crosses Marico x SST 822, Marico x Olifants and Kariega x SST 806 had the highest NHI values at the LN treatment. Steenbras x SST 822, SST 806 x Inia and Marico x SST 806 had the highest values at HN. On average, the crosses Olifants x SST 806, Marico x Olifants and SST 806 x SST 822 showed the highest NHI values. The tested genotypes showed genetic variability for NHI due to the two N treatments.

4.7.6.3 Calculated Nitrogen use efficiency components

Nitrogen uptake efficiency

Nitrogen uptake efficiency is calculated as the total N uptake by the crop as a percentage of available N (fertilizer and soil mineral N) to the crop. The calculated N uptake efficiency values (NupE%) presented in Table 4.9, show an overall mean of 74.79% for the trial planted at Bethlehem. The NupE% was significantly reduced from 88.73% to 60.85% at the HN treatment. The parental cultivars showed significant differences in response to the two N treatments. Inia, SST 806 and Olifants had the highest values at the LN treatment, with the cultivars Marico, Kariega and Olifants showing the highest values at the HN treatment. Inia was the parent with the highest mean NupE% value of 78.75%, with only SST 822 significantly lower at 61.59%.

The cross SST 806 x SST 822 had the highest value at the LN treatment, followed by Marico x SST 822, Kariega x Steenbras and Marico x Steenbras. The crosses Olifants x Steenbras, Kariega x Olifants and Marico x SST 806 had the highest values at the HN treatment. Averaged over N treatments, the crosses SST 806 x SST 822, Marico x SST 822 and Marico x SST 806 had the highest NupE% values. The crosses SST 806 x Inia, Kariega x SST 822 and Kariega x SST 806 had the lowest mean NupE% values. These crosses showed the smallest response for NupE% due to the HN treatment. Several of the values calculated were above 100%, indicating the contributing effect of the residual soil mineral N to the N uptake and accumulation by the plant.

Nitrogen use efficiency for grain yield

The calculated NUE results for grain yield (NUEYld) is the grain yield (kg) harvested per available N (kg) to the crop. The wheat trial at Bethlehem showed a mean of 27.63 kg yield/kg N. The N treatments showed significant responses with the NUEYld values reduced from 35.29 kg/kg N at the LN treatment to 19.96 kg/kg N at the HN treatment. This decrease in NUEYld in response to N application was also noted by Soon *et al.* (2006). The parental cultivars also showed significant response to the N treatments. The parent SST 806 had the highest value of 41.90 kg/kg N at the LN treatment, followed by Inia, Kariega and Olifants with Steenbras and SST 822 at significantly lower values. At the HN treatment, the cultivars Marico, Kariega and Olifants had the best responses. Inia was the parent with the highest mean NUEYld value of 29.98 kg/kg N, with Steenbras and SST 822 significantly lower.

The cross SST 806 x SST 822 had the highest value at the LN treatment, followed by Marico x SST 822, and Kariega x Steenbras. Marico x SST 806 was the cross with the

Table 4.9 Mean Nitrogen use efficiency components for seven parental cultivars and their F_2-offspring planted at Bethlehem at two N treatments in 2004

Genotypes	NupE%[a]			NUEYld[b]			NutEYld[c]			AEGP[d]	NAEYld[e]	NPE[f]	NRE[g]
	LN	HN	Mean	LN	HN	Mean	LN	HN	Mean	Mean	Mean	Mean	Mean
Kariega	86.66	64.93	75.80	36.96	22.59	29.77	42.92	34.72	38.82	0.009	13.140	23.450	50.640
Marico	80.77	66.95	73.86	30.97	23.46	27.22	38.04	35.02	36.53	0.009	18.520	31.600	57.870
Olifants	90.56	63.40	76.98	36.80	21.10	28.95	40.51	33.14	36.82	0.013	15.230	27.060	54.430
Steenbras	89.87	54.07	71.97	31.15	16.57	23.86	34.67	30.86	32.76	0.006	9.490	31.240	30.340
SST 806	97.86	50.26	74.06	41.90	17.94	29.92	42.84	35.73	39.29	0.006	4.060	17.410	23.290
SST 822	71.12	52.07	61.59	28.23	16.70	22.47	40.06	32.68	36.37	0.014	9.120	22.710	39.550
Inia	103.60	53.90	78.75	41.27	18.68	29.98	39.65	34.56	37.11	0.008	9.040	25.820	31.580
Kariega x Marico	97.38	58.17	77.78	41.00	17.32	29.16	43.19	29.83	36.51	0.013	-1.670	-7.010	23.550
Kariega x Olifants	81.99	71.59	76.79	32.56	21.39	26.97	40.04	30.20	35.12	0.015	14.040	21.450	64.760
Kariega x Steenbras	103.76	55.79	79.78	44.71	17.23	30.97	43.33	30.81	37.07	0.016	2.630	5.690	32.380
Kariega x SST 806	69.05	66.21	67.63	28.55	20.90	24.72	41.90	31.58	36.74	0.009	15.860	25.340	64.340
Kariega x SST 822	71.04	63.01	67.03	28.68	20.57	24.63	40.52	32.26	36.39	0.012	19.410	29.900	64.950
Kariega x Inia	84.76	56.65	70.71	34.56	17.96	26.26	40.51	31.77	36.14	0.007	12.320	25.560	49.550
Marico x Olifants	95.11	64.43	79.77	41.90	21.31	31.61	44.63	33.14	38.88	0.010	12.620	22.440	55.240
Marico x Steenbras	102.66	49.73	76.20	42.00	15.17	28.58	41.07	30.32	35.69	0.013	-0.770	-15.710	17.130
Marico x SST 806	96.95	70.05	83.50	35.69	25.50	30.60	36.37	36.46	36.41	0.008	23.810	35.340	65.960
Marico x SST 822	106.93	66.74	86.84	44.49	19.73	32.11	41.98	29.82	35.90	0.013	3.440	7.640	40.310
Marico x Inia	85.11	57.90	71.50	28.91	19.75	24.33	33.46	34.33	33.89	0.007	18.960	32.000	52.480
Olifants x Steenbras	87.00	72.49	79.74	31.08	23.32	27.20	35.30	32.09	33.70	0.012	18.220	28.010	62.940
Olifants x SST 806	82.68	64.61	73.64	33.62	22.04	27.83	40.53	34.08	37.31	0.008	18.900	32.650	57.880
Olifants x SST 822	94.96	54.45	74.71	36.53	16.57	26.55	38.88	30.46	34.67	0.016	4.890	13.680	35.690
Olifants x Inia	86.24	64.77	75.50	34.43	21.24	27.84	39.86	32.67	36.26	0.016	12.570	23.170	50.650
Steenbras x SST 806	90.21	58.42	74.32	34.91	19.28	27.09	39.15	33.10	36.13	0.008	11.000	23.230	44.180
Steenbras x SST 822	91.49	69.28	80.38	33.24	23.84	28.54	36.23	34.41	35.32	0.007	17.670	32.220	54.660
Steenbras x Inia	81.28	54.85	68.07	33.27	17.32	25.29	41.03	31.40	36.22	0.014	11.300	22.460	49.450
SST 806 x SST 822	112.50	67.79	90.14	45.00	23.03	34.01	40.05	33.88	36.96	0.010	12.470	26.860	45.050
SST 806 x Inia	64.82	50.53	57.67	25.78	17.88	21.83	39.76	35.37	37.57	0.013	12.690	32.870	41.140
SST 822 x Inia	78.06	60.63	69.34	29.99	20.60	25.30	38.83	33.90	36.36	0.007	14.430	28.620	49.170
Mean	**88.73a**	**60.85b**	**74.79**	**35.29a**	**19.96b**	**27.63**	**39.83a**	**32.81b**	**36.32**	**0.011**	**11.910**	**22.350**	**46.760**

[a]NupE%: Nitrogen uptake efficiency; [b]NUEYld; Nitrogen use efficiency for grain yield; [c]NutEYld: Nitrogen utilization efficiency for grain yield; [d]AEGP:Agronomic efficiency for grain protein; [e]NAEYld: Agronomic efficiency for grain yield; [f]NPE:Physiological efficiency; [g]NRE: Recovery efficiency.

LSD (0.05)	24.37	12.03	13.43	10.01	4.78	5.52	6.12	4.01	ns	0.005	7.824	9.278	21.28
LSD (0.05) G x N			23.04			8.21			5.50				
CV%			15.70%			17.50%			8.70%	29.60%	40.10%	25.40%	27.80%

highest value at the HN treatment, followed by Steenbras x SST 822 and Olifants x Steenbras. Averaged over N treatments, the cross SST 806 x SST 822 had the highest value, followed by Marico x SST 822 and Marico x Olifants. SST 806 x Inia had the lowest NUEYld value, followed by Marico x Inia and Kariega x SST 822. The generally higher NUEYld values at the LN treatment indicate that certain genotypes are able to exploit the soil profile more efficiently probably via extended root systems, or more efficient internal use of N taken up to produce grain yield.

Nitrogen utilization efficiency for grain yield

The calculated results of N utilization efficiency for grain yield (NutEYld) is expressed as the grain yield that the plant was capable of producing per kg N that was previously acquired and stored in the aboveground biomass. A mean of 36.32 kg grain yield per kg N taken up by the plant was calculated for the trial planted at Bethlehem. The N treatment significantly decreased the NutEYld values from 39.83 kg grain yield/kg N at the LN treatment to 32.81 kg grain yield/kg N at the HN treatment. Although the averaged values for the genotypes did not differ significantly, significant differences were calculated for the response at the respective N treatments. The parents Kariega (42.92 kg/kg N) and SST 806 (42.84 kg/kg N) had the highest values at the LN treatment, but only SST 822 had a significantly lower value. Similarly, at the HN treatment SST 806, Marico and Kariega had the highest values, with SST 822 significantly lower.

The crosses Marico x Olifants, Kariega x Steenbras and Kariega x Marico had the highest values at the LN treatment. The crosses Marico x SST 806, SST 806 x Inia and Steenbras x SST 822 showed the best responses at the HN treatment. The response of the genotypes at the LN treatment highlights increased internal efficiency of N use in these plants when available N is restricted. The cultivar SST 806 showed the ability to effectively use N at both the low and high N availability treatments.

Agronomic efficiency for grain protein

The calculated agronomic efficiency for increase in grain protein (%) per kg N applied (HN treatment) above the control (LN treatment) (AEGP) had a mean value of 0.011% per kg N. The parental cultivars showed significant differences with SST 822 at the highest value of 0.014 %/kg N, with only SST 806, and Steenbras that had significant lower values. The crosses Olifants x Inia, Olifants x SST 822, Kariega x Steenbras and Kariega x Olifants had high AEGP values. SST 822 x Inia, Kariega x Inia, Steenbras x SST 822 and Marico x Inia had the lowest values for AEGP.

Agronomic efficiency for grain yield

The agronomic efficiency for grain yield (NAEYld) calculates the increase in grain yield at the HN treatment compared to the LN treatment, and in the wheat trial planted at Bethlehem this increase in grain yield in response to N application showed a mean value of 11.91 kg/kg N. The parental cultivars differed significantly with Marico, Olifants and Kariega showing significantly higher values. The responses of these cultivars also indicate their higher grain yield to applied N measured at the HN treatment, and lower grain yields at the LN treatment. The crosses Marico x SST 806, Kariega x SST 822 and Marico x Inia showed the highest NAEYld values. The lowest NAEYld values were calculated for the crosses Kariega x Marico, Marico x Steenbras and Kariega x Steenbras.

Physiological efficiency

Physiological efficiency (NPE) is calculated as the difference in the increase in grain yield per kg N taken up by the plant between the fertilized (HN) and control (LN) treatments. This is an indication of the ability of a genotype to effectively utilize N previously taken up into the biomass to produce harvestable grain yield. The results as shown in Table 4.9 indicate a mean of 22.35 kg/kg N for the wheat trial at Bethlehem. The parental cultivars differed significantly and SST 806 showed a significantly lower value (17.41 kg/kg N) compared to the highest value found at Marico (31.60 kg/kg N) and Olifants, with SST 822 significantly lower. The crosses Marico x SST 806, SST 806 x Inia and Olifants x SST 806 had the highest NPE values. The cross Marico x Steenbras had the lowest NPE value, followed by Kariega x Marico and Kariega x Steenbras. The high NutEYld value for SST 806 discussed previously, combined with the high grain yield of this cultivar at the LN treatment, resulted in a low NPE value because of the difference method of calculating NPE.

Recovery efficiency

Recovery efficiency (NRE) is the difference in total N uptake between the HN and LN treatments as a percentage of applied fertilizer N. The calculated NRE results showed a mean value of 46.76% for the wheat trial at Bethlehem. The genotypes differed significantly with the highest values at Marico (57.87%), Olifants (54.43%) and Kariega (50.64%). These cultivars also had the high biomass, Ntotal and NupE% values at the HN treatment, combining to increase the sink/source relationship and hence higher total N uptake. The crosses Marico x SST 806, Kariega x SST 822 and Kariega x Olifants showed the highest NRE values. Low NRE values were calculated for Marico x Steenbras, Kariega x Marico, and Kariega x Steenbras. The tested genotypes showed genetic variation for NRE indicating that certain genotypes are more efficient in accumulating N in the aboveground biomass, which is probably linked to the sink/source relationship of the plant, and differences in root system development and effectivity.

4.7.7 Tables of means: Vaalharts

4.7.7.1 Measured agronomic characteristics

The results of the measured agronomic characteristics, N uptake measurements and calculated NUE components in the 2004 trial for Vaalharts are listed in Tables 4.10, 4.11 and 4.12 respectively.

Biomass

The mean biomass at harvest (BM) was 896.8 g/m^2 (Table 4.10) for the wheat trial planted at Vaalharts. Biomass was significantly increased from 516.9 g/m^2 at the LN treatment to 1276.7 g/m^2 at the HN treatment. The parental cultivars showed significant differences for BM in response to the N treatments. The parental cultivar SST 822 had the highest BM of 632.5 g/m^2 at the LN treatment, not significantly different from SST 806 and Olifants. SST 806 produced the highest BM (1727.3 g/m^2) at the HN treatment. Its BM was significantly higher than the other parental cultivars. This can be ascribed to the specific plant ideotype of SST 806 that includes genes for lodging tolerance.

The crosses Kariega x Olifants, Kariega x SST 806 and Olifants x Steenbras produced the highest BM at the LN treatment, with Olifants x Inia, SST 806 x SST 822 and Kariega x Inia with the highest BM values at the HN treatment.

Grain yield

The mean grain yield for the genotypes planted at Vaalharts was lower compared to Bethlehem at 2.839 t/ha, in part due to the particularly low yields measured at the LN treatment (1.904 t/ha), with a significant yield response to the HN treatment (3.774 t/ha). The parental cultivars and their F_2-offspring responded significantly to the HN treatment. SST 822, SST 806 and Steenbras had the highest yields at the LN treatment. These cultivars yielded significantly higher than Marico. Olifants, SST 806, Inia and SST 822 had the highest yields at the HN treatment, significantly higher than Steenbras.

The cross Steenbras x SST 822 had the highest yield at the LN treatment (2.567 t/ha), followed by Kariega x Olifants, and Olifants x Steenbras. Olifants x Inia, Kariega x Inia and Steenbras x SST 806 responded with the highest yields at the HN treatment. The below average yield recorded (in particular at the LN treatment) is due to the low

Table 4.10 Mean agronomic characteristics for seven parental cultivars and their F_2 -offspring planted at Vaalharts at two N treatments in 2004

Genotypes	BM[a]			Yld[b]			HM[c]			TKM[d]			GP[e]			HI[f]		
	LN	**HN**	**Mean**	**LN**	**HN**	**Mean**	**LN**	**HN**	**Mean**	**LN**	**HN**	**Mean**	**LN**	**HN**	**Mean**	**LN**	**HN**	**Mean**
Kariega	496.3	1134.5	815.4	1.830	2.901	2.365	77.37	74.23	75.80	28.40	24.23	26.32	10.15	11.99	11.07	0.366	0.260	0.313
Marico	428.2	1265.3	846.8	1.436	3.448	2.442	74.77	72.53	73.65	23.73	20.07	21.90	10.48	11.19	10.83	0.335	0.274	0.305
Olifants	517.3	1354.2	935.8	1.791	4.847	3.319	73.03	72.80	72.92	20.67	20.27	20.47	10.29	12.09	11.19	0.346	0.377	0.362
Steenbras	354.4	938.0	646.2	1.981	1.841	1.911	76.53	72.77	74.65	24.27	20.20	22.23	10.32	11.56	10.94	0.600	0.200	0.400
SST 806	578.5	1727.3	1152.9	2.126	4.468	3.297	76.33	73.03	74.68	24.47	20.60	22.53	10.22	11.92	11.07	0.367	0.258	0.313
SST 822	632.5	1204.9	918.7	2.211	3.722	2.967	76.33	73.70	75.02	26.20	23.40	24.80	10.68	11.71	11.20	0.357	0.309	0.333
Inia	438.5	1273.8	856.1	1.673	4.295	2.984	75.87	74.17	75.02	25.73	23.27	24.50	10.29	12.27	11.28	0.379	0.340	0.360
Kariega x Marico	516.4	968.0	742.2	1.847	2.285	2.066	75.50	73.67	74.58	25.73	21.77	23.75	10.19	12.45	11.32	0.356	0.236	0.296
Kariega x Olifants	729.0	1296.6	1012.8	2.459	3.863	3.161	77.23	75.23	76.23	28.20	24.60	26.40	10.13	11.53	10.83	0.337	0.301	0.319
Kariega x Steenbras	473.9	1046.9	760.4	1.523	2.625	2.074	76.57	73.17	74.87	27.00	20.93	23.97	10.35	12.18	11.27	0.331	0.251	0.291
Kariega x SST 806	702.9	1269.7	986.3	2.125	3.692	2.909	78.07	74.43	76.25	29.60	23.13	26.37	10.46	11.62	11.04	0.312	0.291	0.302
Kariega x SST 822	571.3	1323.0	947.1	2.244	3.686	2.965	78.43	74.63	76.53	30.27	25.60	27.93	10.30	12.34	11.32	0.393	0.282	0.338
Kariega x Inia	565.7	1479.6	1022.6	2.143	4.468	3.306	77.63	76.37	77.00	27.33	26.60	26.97	10.23	12.36	11.30	0.386	0.304	0.345
Marico x Olifants	473.1	1359.1	916.1	1.733	3.499	2.616	74.77	71.60	73.18	23.73	20.13	21.93	10.11	12.25	11.18	0.369	0.256	0.313
Marico x Steenbras	561.7	1225.8	893.8	2.099	3.746	2.922	76.57	73.60	75.08	26.27	20.27	23.27	9.82	11.99	10.91	0.372	0.306	0.339
Marico x SST 806	377.4	1349.7	863.5	1.196	3.994	2.595	75.30	72.93	74.12	25.27	21.27	23.27	9.94	12.17	11.06	0.330	0.298	0.314
Marico x SST 822	497.9	1433.7	965.8	1.714	4.576	3.145	76.03	74.83	75.43	26.07	23.87	24.97	9.84	11.74	10.79	0.341	0.320	0.331
Marico x Inia	371.2	1301.2	836.2	1.440	4.234	2.837	73.97	73.43	73.70	22.27	21.40	21.83	10.50	12.39	11.45	0.391	0.331	0.361
Olifants x Steenbras	650.2	1426.0	1038.1	2.436	3.834	3.135	75.17	72.37	73.77	23.27	19.47	21.37	10.52	11.69	11.11	0.380	0.272	0.326
Olifants x SST 806	551.1	1276.0	913.5	1.955	3.854	2.904	73.90	72.60	73.25	22.20	19.87	21.03	10.82	11.77	11.30	0.357	0.300	0.329
Olifants x SST 822	345.1	1105.9	725.5	1.333	3.729	2.531	74.80	74.07	74.43	23.87	22.53	23.20	10.39	12.54	11.47	0.386	0.350	0.368
Olifants x Inia	575.1	1762.1	1168.6	2.197	5.260	3.729	75.33	73.73	74.53	24.80	21.93	23.37	10.12	11.93	11.02	0.383	0.300	0.342
Steenbras x SST 806	596.0	1319.9	957.9	2.060	4.540	3.300	78.40	74.90	76.65	30.27	22.67	26.47	10.04	11.87	10.95	0.345	0.342	0.344
Steenbras x SST 822	551.4	1028.2	789.8	2.567	3.187	2.877	75.67	73.70	74.68	25.33	21.87	23.60	10.12	12.33	11.23	0.491	0.308	0.400
Steenbras x Inia	505.0	1258.6	881.8	2.059	3.702	2.881	76.90	75.33	76.12	27.27	25.60	26.43	10.37	12.25	11.31	0.407	0.295	0.351
SST 806 x SST 822	567.7	1498.7	1033.2	2.076	4.326	3.201	75.57	74.60	75.08	25.13	23.53	24.33	10.11	12.35	11.23	0.366	0.288	0.327
SST 806 x Inia	492.8	1148.0	820.4	1.822	3.466	2.644	76.90	74.83	75.87	27.53	23.87	25.70	9.96	11.73	10.85	0.369	0.301	0.335
SST 822 x Inia	352.7	972.7	662.7	1.244	3.595	2.420	75.80	74.80	75.30	25.60	24.73	25.17	10.70	13.02	11.86	0.353	0.376	0.365
Mean	**516.9a**	**1276.7b**	**896.8**	**1.904a**	**3.774b**	**2.839**	**76.03a**	**73.86b**	**74.94**	**25.73a**	**22.42b**	**24.07**	**10.27a**	**12.04b**	**11.16**	**0.375a**	**0.297b**	**0.336**
LSD (0.05)	169.6	318.6	178.4	0.571	0.852	0.507	ns	ns	1.97	ns	3.72	3.17	ns	ns	ns	0.107	0.077	ns
LSD (0.05) G x N			253.6			0.727			ns			ns			ns			0.091
CV%			17.40%			15.60%			2.30%			11.50%			4.40%			16.90%

[a] BM: Biomass; [b] Yld: Grain yield; [c] HM: Hectoliter mass; [d] TKM: Thousand kernel mass; [e] GP: Grain protein percentage; [f] HI: Harvest index.

residual soil mineral N measured at planting, and linked to the limited N availability during the growing season due to N immobilization by decomposing crop residue. The application of N increased grain yields of all the genotypes as was found by Soon *et al*. (2006).

Hectoliter mass

The mean hectoliter mass (HM) for the wheat trial planted at Vaalharts was 74.94 kg/hl, and similarly to Bethlehem, the HN treatment resulted in negative responses in HM values. The genotypes tested responded negatively for HM to the HN treatment, although the Genotype x N treatment interactions did not differ significantly. The parental cultivar Kariega had the highest HM at both N treatments, followed by SST 822 and Inia. Olifants and Marico had significantly lower mean HM values. The cross Kariega x Inia had the highest mean HM, not significantly different from Steenbras x SST 806, Kariega x SST 822 and Kariega x SST 806.

Thousand kernel mass

The mean thousand kernel mass (TKM) for the trial planted at Vaalharts was 24.07 g, which is significantly lower compared to the trial at Bethlehem. The measured TKM was significantly lower for the HN (22.42 g) compared to the LN treatment (25.73 g). No significant differences were found in the interaction between genotypes at both the LN and HN treatments. Similarly, to the response found at HM, the parent Kariega had the highest mean TKM of 26.32 g, followed by SST 822 and Inia. The cross Kariega x SST 822 had the highest mean TKM value of 27.93 g, followed by Kariega x Inia and Steenbras x SST 806.

Grain protein percentage

The mean grain protein percentage (GP) of the Vaalharts trial was 11.10%. The N application significantly increased the mean GP from 10.27% at the LN treatment to 12.04% at the HN treatment. The parental cultivars and crosses did not differ significantly in GP at the respective N treatments or in mean values. This indicates that the genotypes responded correspondingly to the HN treatment with increased GP values.

Harvest index

The mean harvest index (HI) for Vaalharts was 0.336 (Table 4.10). The HN treatment (0.297) significantly reduced HI compared to the LN treatment (0.375). This points out that the increased N fertility increased biomass development of the genotypes at the HN treatment, but that the grain yield was not increased proportionately compared to the LN treatment. The parental cultivars differed significantly in HI values in response to the N treatments. The parental cultivar Steenbras had the highest value of 0.600 at the LN treatment, followed by Inia and SST 806. At the HN treatment, Olifants had the highest HI value (0.377), not significantly different from Inia and SST 822.

The crosses Steenbras x SST 822, Steenbras x Inia and Kariega x SST 822 had the highest HI values at the LN treatment. The crosses SST 822 x Inia, Olifants x SST 822 and Steenbras x SST 806 showed the highest values at the HN treatment. The genotypes where a parental cultivar with reduced height characteristics was used (SST 822) showed increased HI values at both N treatments

4.7.7.2 Measured Nitrogen uptake and calculated components

Nitrogen uptake in the grain

The mean N uptake of the grain (Ngrain) showed a value of 57.02 kg N/ha for the trial planted at Vaalharts (Table 4.11). The genotypes responded significantly to N application with the HN treatment at a higher value of 79.78 kg N/ha compared to 34.27 kg N/ha at the LN treatment. Significant differences were found between the parental cultivars for Ngrain at both the N treatments. The parental cultivar SST 822 showed the highest Ngrain value of 41.23 kg N/ha at the LN treatment, not significantly different from SST 806 and Steenbras. Olifants, SST 806 and Inia in turn had the highest values at the HN treatment.

The crosses Steenbras x SST 822, Olifants x Steenbras and Kariega x Olifants showed the highest values for Ngrain at the LN treatment. Olifants x Inia, Kariega x Inia and Marico x SST 822 displayed the highest values at the HN treatment. Olifants x Inia, Kariega x Inia, Steenbras x SST 806 and SST 806 x SST 822 did not differ significantly, and had the highest mean Ngrain values of the genotypes.

Total Nitrogen uptake

The calculated mean total N uptake at harvest (Ntotal) for the trial planted at Vaalharts was 82.27 kg N/ha (Table 4.11). Nitrogen application significantly increased mean N uptake of the tested genotypes from 44.12 kg N/ha at the LN treatment to 120.42 kg N/ha at the HN treatment. The parental cultivars responded significantly to the N treatments. The parental cultivar SST 822 had the highest Ntotal value of 57.64 kg N/ha at the LN treatment, followed by SST 806 and Olifants. SST 806, Olifants and Inia showed highest values at the HN treatment.

Table 4.11 Mean Nitrogen uptake and calculated components for seven parental cultivars and their F_2-offspring planted at Vaalharts at two N treatments in 2004

Genotypes	Ngrain[a]			Ntotal[b]			NHI[c]		
	LN	**HN**	**Mean**	**LN**	**HN**	**Mean**	**LN**	**HN**	**Mean**
Kariega	32.34	61.22	46.78	41.85	99.66	70.75	0.772	0.615	0.694
Marico	26.45	67.91	47.18	35.60	109.37	72.49	0.742	0.622	0.682
Olifants	32.34	102.96	67.65	42.06	135.60	88.83	0.772	0.759	0.765
Steenbras	35.90	37.13	36.52	41.76	78.95	60.36	0.861	0.473	0.667
SST 806	38.19	93.12	65.65	47.82	146.96	97.39	0.798	0.633	0.715
SST 822	41.23	76.43	58.83	57.64	115.93	86.79	0.723	0.664	0.694
Inia	30.15	92.92	61.54	38.43	130.21	84.32	0.783	0.716	0.750
Kariega x Marico	32.95	50.16	41.56	42.45	90.67	66.56	0.775	0.554	0.664
Kariega x Olifants	43.57	78.10	60.83	55.84	112.98	84.41	0.782	0.696	0.739
Kariega x Steenbras	27.66	55.76	41.71	38.17	97.91	68.04	0.728	0.576	0.652
Kariega x SST 806	38.95	75.22	57.09	51.26	109.62	80.44	0.759	0.686	0.722
Kariega x SST 822	40.63	79.70	60.17	49.52	125.81	87.67	0.821	0.635	0.728
Kariega x Inia	38.49	96.84	67.66	49.56	148.77	99.16	0.779	0.660	0.719
Marico x Olifants	30.73	74.51	52.62	40.33	121.97	81.15	0.761	0.610	0.686
Marico x Steenbras	36.09	78.97	57.53	46.80	122.04	84.42	0.770	0.649	0.709
Marico x SST 806	20.92	85.36	53.14	27.97	130.56	79.26	0.757	0.653	0.705
Marico x SST 822	29.73	94.56	62.15	38.07	134.17	86.12	0.775	0.701	0.738
Marico x Inia	26.47	92.13	59.30	34.28	131.33	82.81	0.773	0.701	0.737
Olifants x Steenbras	44.97	78.84	61.91	58.16	124.71	91.43	0.778	0.637	0.707
Olifants x SST 806	37.22	79.73	58.47	47.00	111.69	79.35	0.796	0.711	0.754
Olifants x SST 822	24.31	82.28	53.29	30.07	110.90	70.48	0.807	0.744	0.775
Olifants x Inia	38.90	110.09	74.50	49.84	156.11	102.97	0.781	0.708	0.745
Steenbras x SST 806	36.21	94.51	65.36	46.57	132.93	89.75	0.775	0.708	0.742
Steenbras x SST 822	45.57	69.05	57.31	55.80	106.43	81.11	0.819	0.650	0.735
Steenbras x Inia	37.25	79.56	58.40	48.48	126.34	87.41	0.768	0.631	0.699
SST 806 x SST 822	36.75	93.53	65.14	47.32	146.03	96.68	0.775	0.640	0.708
SST 806 x Inia	32.10	71.32	51.71	41.34	101.88	71.61	0.776	0.699	0.737
SST 822 x Inia	23.35	81.98	52.66	31.31	112.30	71.80	0.746	0.726	0.736
Mean	**34.27a**	**79.78b**	**57.02**	**44.12a**	**120.42b**	**82.27**	**0.7768a**	**0.6592b**	**0.718**

[a]Ngrain: Nitrogen uptake in the grain; [b]Ntotal: Total Nitrogen uptake; [c]NHI: Nitrogen harvest index.

LSD (0.05)	10.25	19.20	10.76	12.96	27.39	14.98	ns	0.085	0.054
LSD (0.05) G x N			15.55			21.77			0.075
CV%			16.50%			15.90%			6.60%

Significant differences were found in Ntotal for the crosses, with Olifants x Steenbras, Kariega x Olifants and Steenbras x SST 822 showing the highest values at the LN treatment. Olifants x Inia, Kariega x Inia and SST 806 x SST 822 had the highest values at the HN treatment.

Nitrogen harvest index

The mean N harvest index (NHI) for the wheat trial planted at Vaalharts was 0.718 (Table 4.11). The N application significantly decreased mean NHI from 0.7768 at the LN treatment to 0.6592 at the HN treatment. Both the parental cultivars and their F_2-offspring responded negatively to the higher N treatment for NHI. This was probably caused by the negative correlation between grain protein and grain yield expected at the higher N application, because grain yield was increased preferably to grain protein. Significant differences were found between the parental cultivars for NHI. Steenbras, SST 806 and Inia had the highest NHI values at the LN treatment. Olifants was the parental cultivar with the highest NHI at the HN treatment, followed by Inia and SST 822.

The crosses Kariega x SST 822, Steenbras x SST 822 and Olifants x SST 822 showed the highest NHI values at the LN treatment. Olifants x SST 822, SST 822 x Inia and Olifants x SST 806 had the highest values at the HN treatment. Baeckström *et al*. (2006) found NHI values of 44% and 49% for a conventional and organic system respectively for winter wheat, and 49% and 39% for spring wheat in the respective systems.

4.7.7.3 Calculated Nitrogen use efficiency components

Nitrogen uptake efficiency

Nitrogen uptake efficiency (NupE%) is calculated as the total N uptake by the crop as a percentage of available N to the crop. The calculated N uptake efficiency values for the trial planted at Vaalharts showed a mean of 51.41% (Table 4.12). The NupE% was significantly reduced from 56.23% at the LN treatment to 46.59% at the HN treatment. The parental cultivars and their F_2-offspring responded significantly negatively to the HN treatment. This is probably due to reduced growth of the genotypes or a more effectively developed root system that forced the plants to increase NupE%.

Significant differences were found between the parental cultivars at both low and high N treatments. The cultivar SST 822 performed best at the LN treatment (73.46%), followed by SST 806 (60.95%). Their NupE% values were significantly higher than the other cultivars. The cultivar SST 806 had the highest value (56.86%) at the HN treatment, not significantly different from Olifants and Inia.

Table 4.12 Mean Nitrogen use efficiency components for seven parental cultivars and their F_2-offspring planted at Vaalharts at two N treatments in 2004

Genotypes	NupE%[a]			NUEYld[b]			NutEYld[c]			AEGP[d]	NAEYld[e]	NPE[f]	NRE[g]
	LN	HN	Mean	LN	HN	Mean	LN	HN	Mean	Mean	Mean	Mean	Mean
Kariega	53.34	38.56	45.95	23.33	11.22	17.27	43.44	29.25	36.34	0.010	5.950	17.880	32.120
Marico	45.38	42.32	43.85	18.30	13.34	15.82	40.35	31.75	36.05	0.004	11.180	27.530	40.980
Olifants	53.60	52.46	53.03	22.82	18.75	20.79	43.12	35.70	39.41	0.010	16.980	32.730	51.970
Steenbras	53.23	30.55	41.89	25.24	7.12	16.18	47.54	23.46	35.50	0.007	-0.780	-3.900	20.660
SST 806	60.95	56.86	58.91	27.09	17.29	22.19	44.56	30.41	37.48	0.009	13.010	23.880	55.080
SST 822	73.46	44.86	59.16	28.19	14.40	21.29	38.91	32.52	35.71	0.006	8.390	27.400	32.390
Inia	48.98	50.38	49.68	21.32	16.62	18.97	43.38	33.38	38.38	0.011	14.570	29.280	50.990
Kariega x Marico	54.10	35.08	44.59	23.54	8.84	16.19	43.38	25.41	34.40	0.013	2.430	9.520	26.790
Kariega x Olifants	71.18	43.71	57.44	31.34	14.94	23.14	43.99	34.41	39.20	0.008	7.800	23.850	31.740
Kariega x Steenbras	48.65	37.88	43.26	19.42	10.16	14.79	40.07	27.34	33.71	0.010	6.120	19.270	33.190
Kariega x SST 806	65.34	42.41	53.88	27.09	14.28	20.69	41.38	33.68	37.53	0.006	8.710	27.060	32.420
Kariega x SST 822	63.12	48.68	55.90	28.60	14.26	21.43	45.46	29.33	37.39	0.011	8.010	18.840	42.380
Kariega x Inia	63.17	57.56	60.36	27.32	17.29	22.30	43.38	30.58	36.98	0.012	12.920	24.110	55.110
Marico x Olifants	51.40	47.19	49.29	22.08	13.54	17.81	42.92	28.59	35.76	0.012	9.810	21.070	45.360
Marico x Steenbras	59.65	47.22	53.43	26.75	14.49	20.62	44.71	30.87	37.79	0.012	9.150	22.120	41.800
Marico x SST 806	35.65	50.51	43.08	15.24	15.45	15.34	43.92	30.60	37.26	0.012	15.550	27.360	56.990
Marico x SST 822	48.52	51.91	50.22	21.85	17.70	19.77	44.87	33.99	39.43	0.011	15.900	28.780	53.390
Marico x Inia	43.70	50.81	47.25	18.36	16.38	17.37	41.96	32.27	37.11	0.011	15.520	28.790	53.920
Olifants x Steenbras	74.12	48.25	61.19	31.04	14.83	22.94	42.17	31.09	36.63	0.008	10.770	19.490	43.640
Olifants x SST 806	59.91	43.21	51.56	24.91	14.91	19.91	42.07	34.44	38.25	0.005	10.550	28.920	35.940
Olifants x SST 822	38.32	42.91	40.61	16.98	14.43	15.71	44.26	33.77	39.02	0.012	13.320	29.760	44.910
Olifants x Inia	63.52	60.40	61.96	28.01	20.35	24.18	44.04	33.85	38.95	0.010	17.010	28.990	59.040
Steenbras x SST 806	59.35	51.43	55.39	26.25	17.56	21.91	44.02	34.02	39.02	0.010	13.780	28.470	47.980
Steenbras x SST 822	71.11	41.18	56.15	32.71	12.33	22.52	46.10	30.06	38.08	0.013	6.090	17.640	34.530
Steenbras x Inia	61.79	48.88	55.33	26.25	14.32	20.29	42.26	29.35	35.80	0.010	9.120	20.890	43.260
SST 806 x SST 822	60.32	56.50	58.41	26.46	16.74	21.60	43.73	29.63	36.68	0.012	12.500	22.430	54.840
SST 806 x Inia	52.69	39.42	46.06	23.23	13.41	18.32	44.47	33.96	39.22	0.010	5.800	24.730	26.960
SST 822 x Inia	39.90	43.45	41.68	15.85	13.91	14.88	39.74	31.82	35.78	0.013	13.070	28.600	45.000
Mean	**56.23a**	**46.59b**	**51.41**	**24.27a**	**14.6b**	**19.44**	**43.22a**	**31.27b**	**37.25**	**0.010**	**10.473**	**23.410**	**42.621**

[a] NupE%: Nitrogen uptake efficiency; [b] NUEYld; Nitrogen use efficiency for grain yield; [c] NutEYld: Nitrogen utilization efficiency for grain yield; [d] AEGP:Agronomic efficiency for grain protein; [e] NAEYld: Agronomic efficiency for grain yield; [f] NPE:Physiological efficiency; [g] NRE: Recovery efficiency.

LSD (0.05)	16.52	10.60	9.70	7.27	3.30	3.95	5.29	4.97	3.59	ns	5.093	8.314	15.09
LSD (0.05) G x N			13.63			5.49			5.03				
CV%			16.50%			17.70%			8.40%	43.40%	29.70%	21.70%	21.60%

The cross Olifants x Steenbras had the highest value at the LN treatment (74.12%), followed by Kariega x Olifants and Steenbras x SST 822. The cross Olifants x Inia showed the highest value (60.40%) at the HN treatment followed by Kariega x Inia and SST 806 x SST 822. The results reveal sufficient genetic variability for NupE% between the genotypes at both N treatments to improve the NupE% of wheat cultivars significantly. The cultivars with the highest NupE% at the LN treatment did not necessarily had the highest NupE% at the HN treatment, and vice versa. Some cultivars like SST 806 possessed of relatively high NupE% at both N treatments.

Nitrogen use efficiency for grain yield

The calculated NUE for grain yield (NUEYld) results showed a mean of 19.44 kg grain yield per kg N available to the crop for the trial planted at Vaalharts during 2004 (Table 4.12). The N treatments significantly reduced the mean NUEYld of the wheat genotypes from 24.27 kg/kg N at the LN treatment to 14.60 kg/kg N at the HN treatment consistent with results by Soon *et al*. (2006). Significant variability was found between cultivars for NUEYld. At the LN treatment, the parental cultivars SST 822, SST 806 and Steenbras had the highest values, with Marico significantly lower. Olifants was the parent with the highest value (18.75 kg/kg N) at the HN treatment, not significantly different from SST 806 and Inia.

Significant differences for NUEYld were found between the crosses at both N treatments. The crosses Steenbras x SST 822, Kariega x Olifants and Olifants x Steenbras had the highest values at the LN treatment, while Olifants x Inia, Marico x SST 822 and Steenbras x SST 806 had the highest NUEYld values at the HN treatment. The results revealed sufficient genetic variability for NUEYld between the genotypes tested at both N treatments.

Nitrogen utilization efficiency for grain yield

Nitrogen utilization efficiency for grain yield (NutEYld) is expressed as the grain yield (kg) that the plant produced per kg N that was acquired and accumulated in the above ground biomass at harvest. The results had a mean of 37.25 kg/kg N with a significant reduction in NutEYld value with N application. The NutEYld value was reduced from 43.22 kg/kg N at the LN treatment to 31.27 kg/kg N at the HN treatment. Steenbras, SST 806 and Kariega showed the best response at the LN treatment.

Significant differences between the parental cultivars were found at the HN treatment. The cultivar Olifants had the highest NutEYld value (35.70 kg/kg N), with SST 806, Steenbras and Kariega significantly lower. The differences between the crosses were also significant, with the cross Steenbras x SST 822 at the highest value at the LN treatment (46.10 kg/kg N), not significantly different from Kariega x SST 822 and Marico x SST 822. The cross Olifants x SST 806 had the highest value at the HN treatment (34.44 kg/kg N), followed by Kariega x Olifants and Steenbras x SST 806. The results indicate that genetic variability for NutEYld exists between the genotypes tested.

Agronomic efficiency for grain protein

Results for the agronomic efficiency indicating the increase in grain protein (%) per kg N applied (AEGP) showed a mean value of 0.010% per kg N, with the tested genotypes not differing significantly. This indicates that all the genotypes tested responded similarly with increases in grain protein to N application.

Agronomic efficiency for grain yield

Significant differences for agronomic efficiency for the increase in grain yield (NAEYld) with the application of N were calculated for the wheat trial planted at Vaalharts. The mean NAEYld value was 10.473 kg grain per kg N applied. The parental cultivars differed significantly, with the cultivar Olifants with the highest NAEYld value of 16.980 kg/kg N, not significantly different from Inia and SST 806. The cultivar Steenbras had the lowest NAEYld value. The cross Olifants x Inia showed the highest NAEYld value followed by Marico x SST 822, Marico x SST 806 and Marico x Inia.

Physiological efficiency

The calculated physiological efficiency (NPE) indicating the difference in grain yield produced per kg N accumulated in the plant between the LN and HN treatments, showed a mean of 23.410 kg grain per kg N uptake for the trial planted at Vaalharts. The parental cultivars differed significantly in NPE values. The parental cultivars Olifants, Inia, Marico and SST 806 showed the highest values. The crosses differed significantly, with Olifants x SST 822, Olifants x Inia and Olifants x SST 806 at the highest values. The crosses Kariega x Marico, Steenbras x SST 822, Kariega x SST 822 and Kariega x Steenbras showed significantly lower values.

Recovery efficiency

Recovery efficiency (NRE) is the difference between the HN and LN treatments in total N uptake as a percentage of applied fertilizer N. The mean NRE value was 42.621% for the trial planted at Vaalharts. The parental cultivars and their F_2-offspring differed significantly in NRE. The parental cultivar SST 806 had the highest value of 55.080%, not significantly different from Olifants, Inia and Marico. The cross Olifants x Inia had the highest NRE (59.040%), not significantly different from Marico x SST 806, Kariega x Inia, SST 806 x SST 822, Marico x Inia and Marico x SST 822. Baeckström *et al*. (2006) found in a study on wheat systems in Sweden that a conventional system used 74% of available N, in comparison to an organically cultivated crop that used 81%.

4.7.8 Calculated correlation matrixes

The correlation coefficients between all the measured and calculated components were calculated for the LN and HN treatments, and the results for Bethlehem and Vaalharts are presented in Tables 4.13 and 4.14 respectively.

4.7.8.1 Bethlehem

High correlation coefficients were found between biomass and grain yield, Ngrain and Ntotal at the HN treatment (Table 4.13). Biomass showed high correlation coefficients with NupE% and NUEYld at the HN treatment. Biomass showed varied correlations with the NPE, NRE and NAEYld calculated components where the LN treatment resulted in large negative correlation coefficients and the HN treatment in significant positive coefficients. The results reveal that the HN treatment stimulated growth, which increased biomass development, and caused the high relationships between biomass and the parameters associated with increases in biomass. The increase in biomass production measured at harvest, created the sink for N uptake and accumulation in the plant, increasing the available pool of N in the plant for increased growth, translocation to the grain and increasing N concentration of relevant tissues. Low soil mineral N availability limited plant growth at the LN treatment, in particular early in the growing season when root growth is still limited to only a part of the soil profile. This combination of factors reduced the correlation coefficients between biomass and the specified characters.

Grain yield was highly correlated with Ngrain, Ntotal, NupE% and NUEYld at both the LN and HN treatments. These results emphasize the important relationships between grain yield and N related characteristics even at low N applications. The strong relationship between grain yield and NupE% emphasize the importance of a high NupE% which is

Table 4.13 Correlation coefficients between measured and calculated characteristics for a wheat trial planted at Bethlehem in 2004

N level	Component	*BM*[a]		*Yld*[b]		*HM*[c]		*TKM*[d]		*GP*[e]		*HI*[f]		*Ngrain*[g]		*Ntotal*[h]		*NHI*[i]		*NupE%*[j]		*NUEYld*[k]		*NutEYld*[l]		*AEGP*[m]		*NAEYld*[n]		*NPE*[o]		*NRE*[p]
LN	BM	1																																
HN	**BM**	**1**																																
LN	YLD	0.604	**	1																														
HN	**YLD**	**0.770**	**	**1**																														
LN	HM	0.324	**	0.318	**	1																												
HN	**HM**	**0.127**		**0.294**	**	**1**																												
LN	TKM	0.026		0.073		0.467	**	1																										
HN	**TKM**	**0.018**		**0.313**	**	**0.651**	**	**1**																										
LN	GP	-0.179		-0.064		-0.437	**	-0.439	**	1																								
HN	**GP**	**-0.296**	**	**-0.307**	**	**-0.311**	**	**-0.303**	**	**1**																								
LN	HI	-0.380	**	0.493	**	0.044		0.063		0.098		1																						
HN	**HI**	**-0.216**		**0.440**	**	**0.253**	*	**0.446**	**	**-0.052**		**1**																						
LN	Ngrain	0.535	**	0.956	**	0.194		-0.045		0.226	*	0.511	**	1																				
HN	**Ngrain**	**0.739**	**	**0.970**	**	**0.232**	*	**0.257**	*	**-0.072**		**0.440**	**	**1**																				
LN	Ntotal	0.683	**	0.892	**	0.166		-0.096		0.288	**	0.276	*	0.956	**	1																		
HN	**Ntotal**	**0.867**	**	**0.880**	**	**0.068**		**0.054**		**-0.020**		**0.134**		**0.920**	**	**1**																		
LN	NHI	-0.319	**	0.478	**	0.119		0.142		-0.108		0.903	**	0.434	**	0.158		1																
HN	**NHI**	**-0.192**		**0.386**	**	**0.363**	**	**0.488**	**	**-0.097**		**0.851**	**	**0.377**	**	**-0.009**		**1**																
LN	NupE%	0.683	**	0.892	**	0.166		-0.096		0.288	**	0.276	*	0.956	**	1.000	**	0.158		1														
HN	**NupE%**	**0.867**	**	**0.880**	**	**0.068**		**0.054**		**-0.020**		**0.134**		**0.920**	**	**1.000**	**	**-0.009**		**1**														
LN	NUEYld	0.604	**	1.000	**	0.318	**	0.073		-0.064		0.493	**	0.956	**	0.892	**	0.478	**	0.892	**	1												
HN	**NUEYld**	**0.770**	**	**1.000**	**	**0.294**	**	**0.313**	**	**-0.307**	**	**0.440**	**	**0.970**	**	**0.880**	**	**0.386**	**	**0.880**	**	**1**												
LN	NutEYld	-0.122		0.379	**	0.339	**	0.355	**	-0.698	**	0.585	**	0.165		-0.070		0.784	**	-0.070		0.379	**	1										
HN	**NutEYld**	**0.001**		**0.478**	**	**0.443**	**	**0.537**	**	**-0.588**	**	**0.718**	**	**0.350**	**	**0.012**		**0.861**	**	**0.012**		**0.478**	**	**1**										
LN	AEGP	0.125		-0.035		0.360	**	0.271	*	-0.631	**	-0.148		-0.210		-0.213		-0.040		-0.213		-0.035		0.355	**	1								
HN	**AEGP**	**0.141**		**-0.049**		**-0.184**		**-0.202**		**0.331**	**	**-0.223**	*	**0.030**		**0.180**		**-0.336**	**	**0.180**		**-0.049**		**-0.441**	**	**1**								
LN	NAEYld	-0.285	*	-0.541	**	-0.298	**	-0.062		0.110		-0.310	**	-0.493	**	-0.444	**	-0.295	**	-0.444	**	-0.541	**	-0.285	*	-0.222		1						
HN	**NAEYld**	**0.313**	**	**0.476**	**	**0.277**	*	**0.177**		**-0.107**		**0.268**	**	**0.471**	**	**0.362**	**	**0.329**	**	**0.362**	**	**0.476**	**	**0.321**	**	**-0.222**		**1**						
LN	NPE	-0.258	*	-0.537	**	-0.202		-0.009		0.218		-0.344	**	-0.457	**	-0.394	**	-0.352	**	-0.394	**	-0.537	**	-0.396	**	-0.349	**	0.813	**	1				
HN	**NPE**	**0.165**		**0.434**	**	**0.228**	*	**0.265**	*	**-0.082**		**0.408**	**	**0.430**	**	**0.273**	*	**0.462**	**	**0.273**	*	**0.434**	**	**0.423**	**	**-0.349**	**	**0.813**	**	**1**				
LN	NRE	-0.355	**	-0.434	**	-0.229	*	-0.012		-0.036		-0.081		-0.433	**	-0.446	**	-0.057		-0.446	**	-0.434	**	-0.026		0.014		0.864	**	0.569	**	1
HN	**NRE**	**0.370**	**	**0.396**	**	**0.138**		**0.050**		**0.060**		**0.088**		**0.430**	**	**0.421**	**	**0.110**		**0.421**	**	**0.396**	**	**0.057**		**0.014**		**0.864**	**	**0.569**	**	**1**
		BM		***Yld***		***HM***		***TKM***		***GP***		***HI***		***Ngrain***		***Ntotal***		***NHI***		***NupE%***		***NUEYld***		***NutEYld***		***AEGP***		***NAEYld***		***NPE***		***NRE***

[a]BM: Biomass; [b]Yld: Grain yield; [c]HM: Hectoliter mass; [d]TKM: Thousand kernel mass; [e]GP: Grain protein percentage; [f]HI: Harvest index;[g]Ngrain: Nitrogen uptake in the grain; [h]Ntotal: Total Nitrogen uptake; [i]NHI: Nitrogen harvest index;[j]NupE%: Nitrogen uptake efficiency; [k]NUEYld; Nitrogen use efficiency for grain yield; [l]NutEYld: Nitrogen utilization efficiency for grain yield;[m]AEGP:Agronomic efficiency for grain protein; [n]AEYld: Agronomic efficiency for grain yield; [o]NPE:Physiological efficiency; [p]NRE: Recovery efficiency.

Significance (P 0.01) **

Significance (P 0.05) *

probably caused by a well developed en effective root system of the wheat plant. Muurinen *et al*. (2006) found in a study on oat, wheat and barley cultivars that NutEYld was positively correlated with NHI for all species. The authors also found that NupE% and NUE were positively correlated with grain yield.

Thousand Kernel Mass (TKM) and hectoliter mass (HM) were significantly correlated with several of the components but with low correlation coefficients.

Grain protein (GP) was negatively correlated with NutEYld at the HN treatment. Grain protein was positive correlated with AEGP at the HN treatment, but had a negative correlation coefficient at the LN treatment. This indicate that under low N availability, the wheat plant utilizes N taken up by the plant predominantly for grain yield production. However, when sufficient N is available, grain protein increases as N availability approaches the amount required for maximum grain yield once the yield potential is reached (McKenzie *et al*., 2006).

Harvest index (HI) showed positive correlations with NHI and NutEYld (HN treatment), but was negatively correlated with NPE and NAEYld at the LN treatment, and positively correlated at the HN treatment. This point to the positive effect of N application on biomass production and grain yield, and the resultant calculated ratio's. These results correspond to results by Thomason *et al*. (2002) and Muurinen *et al*. (2006) who found that improved HI generally increased NUE values.

The N contained in the grain (Ngrain) was highly correlated with Ntotal, NupE% and NUEYld, as the N contained in the grain is the result of the uptake and translocation processes. The Ngrain showed negative correlation coefficients at the LN treatment and positive correlations at the HN treatment with NAEYld, NPE and NRE.

The total N in the above ground plant (Ntotal) was highly correlated with NupE% and NUEYld as found by Muurinen *et al*. (2006). The Ntotal showed negative correlation coefficients at the LN treatment and positive coefficients at the HN treatment with NAEYld, NPE and NRE, indicating the importance of sink/source relationships in the plant.

The NHI was significantly correlated with NutEYld. The NHI was negatively correlated with NPE and NAEYld at the LN treatment, but positively at the HN treatment. The positive affect of N application on grain yield, grain protein and total N uptake by the plant, also increased the calculated NHI.

Nitrogen uptake efficiency (NupE%) was significantly correlated with NUEYld. The correlations with NAEYld, NPE and NRE were negative at the LN treatment, and positive at the HN treatment indicating that N application increased N uptake and this was converted into yield increases.

Nitrogen use efficiency for yield production (NUEYld) was positively correlated with NPE, NRE and NAEYld at the HN treatment, with negative correlation coefficients at the LN treatment.

Nitrogen utilization efficiency for yield production (NutEYld) showed negative correlation coefficients for NPE and NAEYld at the LN treatment, but a negative correlation at the HN treatment for AEGP and a positive correlation at the LN treatment. Agronomic efficiency for grain yield was positively correlated with NPE and NRE.

4.7.8.2 Vaalharts

Biomass (BM) was significantly correlated with grain yield, Ngrain and Ntotal and NupE% and NUEYld (Table 4.14). The correlation coefficients of BM with NPE, NRE and NAEYld were negative at the LN treatment, but changed to positive correlations at the HN treatment.

Grain yield was positive correlated with Ngrain, Ntotal, NupE% and NUEYld. Grain yield was negatively correlated with NPE, NRE and NAEYld at the LN treatment that changed to positive correlations at the HN treatment. Muurinen *et al*. (2006) reported similar results for three grain crop species.

Hectoliter mass showed a significant correlation with thousand kernel mass (TKM) with low correlation coefficients for the majority of other components. Similarly, TKM showed low correlations with the components included.

Grain protein had a negative correlation with NutEYld at both N treatments, indicating that the increases in grain yield that results in increased NutEYld values, limited grain protein. The grain protein was negatively correlated with AEGP at the LN treatment, but positively correlated at the HN treatment showing the positive effect of N application to increase grain protein percentage.

Table 4.14 Correlation coefficients between measured and calculated characteristics for a wheat trial planted at Vaalharts in 2004

N level	Component	BM[a]		Yld[b]		HM[c]		TKM[d]		GP[e]		HI[f]		Ngrain[g]		Ntotal[h]		NHI[i]		NupE%[j]		NUEYld[k]		NutEYld[l]		AEGP[m]		NAEYld[n]		NPE[o]		NRE[p]
LN	BM	1																														
HN	**BM**	**1**																														
LN	Yld	0.780	**	1																												
HN	**Yld**	**0.737**	**	**1**																												
LN	HM	0.318	**	0.246	*	1																										
HN	**HM**	**0.026**		**0.181**		**1**																										
LN	TKM	0.297	**	0.177		0.930	**	1																								
HN	**TKM**	**0.010**		**0.176**		**0.882**	**	**1**																								
LN	GP	-0.002		-0.084		-0.212		-0.201		1																						
HN	**GP**	**-0.061**		**0.037**		**-0.119**		**-0.016**		**1**																						
LN	HI	-0.358	**	0.249	*	-0.181		-0.238	*	-0.044		1																				
HN	**HI**	**-0.167**		**0.529**	**	**0.210**		**0.231**	*	**0.155**		**1**																				
LN	Ngrain	0.780	**	0.986	**	0.214		0.146		0.079		0.242	*	1																		
HN	**Ngrain**	**0.698**	**	**0.980**	**	**0.154**		**0.168**		**0.229**	*	**0.555**	**	**1**																		
LN	Ntotal	0.862	**	0.944	**	0.200		0.142		0.133		0.090		0.967	**	1																
HN	**Ntotal**	**0.836**	**	**0.867**	**	**0.041**		**0.066**		**0.297**	**	**0.219**		**0.901**	**	**1**																
LN	NHI	-0.203		0.291	**	0.061		0.007		-0.198		0.627	**	0.263	*	0.018		1														
HN	**NHI**	**0.081**		**0.644**	**	**0.290**	**	**0.282**	*	**-0.001**		**0.852**	**	**0.631**	**	**0.243**	*	**1**														
LN	NupE%	0.877	**	0.941	**	0.216		0.157		0.127		0.040		0.963	**	0.998	**	0.007		1												
HN	**NupE%**	**0.836**	**	**0.867**	**	**0.041**		**0.066**		**0.297**	**	**0.219**		**0.901**	**	**1.000**	**	**0.243**	*	**1**												
LN	NUEYld	0.780	**	1.000	**	0.246	*	0.177		-0.084		0.249	*	0.986	**	0.944	**	0.291	**	0.941	**	1										
HN	**NUEYld**	**0.737**	**	**1.000**	**	**0.181**		**0.176**		**0.037**		**0.529**	**	**0.980**	**	**0.867**	**	**0.644**	**	**0.867**	**	**1**										
LN	NutEYld	-0.147		0.250	*	0.150		0.105		-0.711	**	0.471	**	0.138		-0.065		0.827	**	-0.069		0.250	*	1								
HN	**NutEYld**	**0.103**		**0.574**	**	**0.311**	**	**0.262**	*	**-0.402**	**	**0.710**	**	**0.483**	**	**0.103**		**0.915**	**	**0.103**		**0.574**	**	**1**								
LN	AEGP	-0.051		-0.005		0.177		0.175		-0.626	**	-0.046		-0.115		-0.141		0.068		-0.126		-0.005		0.400	**	1						
HN	**AEGP**	**0.002**		**0.099**		**0.158**		**0.224**	*	**0.229**	*	**0.139**		**0.143**		**0.135**		**0.073**		**0.135**		**0.099**		**-0.038**		**1**						
LN	NAEYld	-0.204		-0.351	**	-0.235	**	-0.211		-0.024		-0.284	**	-0.355	**	-0.339	**	-0.105		-0.322	**	-0.351	**	-0.053		0.078		1				
HN	**NAEYld**	**0.520**	**	**0.751**	**	**0.041**		**0.008**		**0.104**		**0.453**	**	**0.752**	**	**0.625**	**	**0.572**	**	**0.625**	**	**0.751**	**	**0.481**	**	**0.078**		**1**				
LN	NPE	-0.102		-0.374	**	-0.209		-0.143		0.169		-0.442	**	-0.345	**	-0.303	**	-0.197		-0.281		-0.374	**	-0.226	*	-0.208		0.789	**	1		
HN	**NPE**	**0.314**	**	**0.599**	**	**0.050**		**0.004**		**0.088**		**0.505**	**	**0.597**	**	**0.410**	**	**0.658**	**	**0.410**	**	**0.599**	**	**0.575**	**	**-0.208**		**0.789**	**	**1**		
LN	NRE	-0.185		-0.223	*	-0.129		-0.110		-0.261	**	-0.160		-0.269	*	-0.277	*	-0.008		-0.262	*	-0.223	*	0.147		0.406	**	0.848	**	0.440	**	1
HN	**NRE**	**0.572**	**	**0.685**	**	**0.076**		**0.091**		**0.098**		**0.284**	*	**0.688**	**	**0.664**	**	**0.359**	**	**0.664**	**	**0.685**	**	**0.286**	*	**0.406**	**	**0.848**	**	**0.440**	**	**1**
		BM		*Yld*		*HM*		*TKM*		*GP*		*HI*		*Ngrain*		*Ntotal*		*NHI*		*NupE%*		*NUEYld*		*NutEYld*		*AEGP*		*NAEYld*		*NPE*		*NRE*

[a]BM: Biomass; [b]Yld: Grain yield; [c]HM: Hectoliter mass; [d]TKM: Thousand kernel mass; [e]GP: Grain protein percentage; [f]HI: Harvest index;[g]Ngrain: Nitrogen uptake in the grain; [h]Ntotal: Total Nitrogen uptake; [i]NHI: Nitrogen harvest index;[j]NupE%: Nitrogen uptake efficiency; [k]NUEYld; Nitrogen use efficiency for grain yield; [l]NutEYld: Nitrogen utilization efficiency for grain yield;[m]AEGP:Agronomic efficiency for grain protein; [n]AEYld: Agronomic efficiency for grain yield; [o]NPE:Physiological efficiency; [p]NRE: Recovery efficiency.

Significance (P 0.01) **
Significance (P 0.05) *

The harvest index (HI) showed positive correlation coefficients with NHI, NUEYld and NutEYld at the HN treatment. The NUEYld and NutEYld components indicate the increases in grain yield that occurred and thereby increased HI. Positive correlations were found with NPE and NAEYld at the HN treatment with negative correlation coefficients at the LN treatment.

The N contained in the harvested grain (Ngrain) showed high correlation coefficients with Ntotal, NupE% and NUEYld at both N treatments, and with NAEYld and NRE at the HN treatment. These components contribute to the N uptake and grain yield of the plant, and in turn, increases the available N accumulated in the plant that can be translocated to the grain. The application of N had a positive effect on the correlation between the components.

The total N taken up by the plant at harvest (Ntotal) was correlated with NupE% and NUEYld. The Ntotal was correlated positively with NPE, NRE and NAEYld at the HN treatment, with these correlations being negative at the LN treatment.

Nitrogen harvest index (NHI) was significantly correlated with NutEYld, showing that increased utilization of N taken up by the plant to increase grain yield, also increased the translocation of N to the grain. Nitrogen harvest index was positively correlated with NPE, NRE and NAEYld at the HN treatment, with low or negative correlations coefficients at the LN treatment.

The Nitrogen uptake efficiency component (NupE%) was positively correlated with NUEYld. The NupE%, NUE for grain yield and NutEYld all showed positive correlations with NPE, NRE and NAEYld at the HN treatment, with negative coefficients at the LN treatment. The NAEYld component was positively correlated with NPE.

Correlation analysis indicated that yield under optimum conditions where N is not limiting is determined mostly by increased biomass production, higher N utilization efficiency and reduced N concentration in crop residue. Improved grain yields of genotypes selected under low N conditions are determined largely by increased HI values and higher N uptake efficiencies (van Ginkel *et al*., 2001). Overall, it appears that N uptake efficiency is more closely correlated with yield and biomass improvement than N utilization efficiency at all levels of N availability. However, N uptake efficiency is better able to predict biological performance, maybe because there is more genetic variability or diversity for this component.

4.8 Conclusions

The two environments where the genotypes were tested differed in climatic conditions (in particular temperatures) during the growing season, and this impacted on measured components. The differences in crop rotation systems had a major effect on the soil mineral N in the profile as measured at planting. This in turn changed the magnitude of responses of measured agronomic and N uptake components (grain yield, grain protein, Ngrain and Ntotal) and NUE components to applied fertilizer N.

From the analysis of variance, the agronomic characteristics (BM, grain yield, HM, TKM and GP) showed significant genotypic variation. Grain yield and GP of the genotypes had significant responses to the HN treatment. Harvest index showed no significant genotypic variation, and BM, HM, TKM and HI any significant response to the HN treatment. The N uptake and NUE components (NAEYld, NPE and NRE) showed significant genotypic variation. The HN treatment resulted in significant variation in Ngrain, Ntotal NHI, NUEYld and NutEYld. The application of N increased BM, grain yield and GP values, but reduced HM, TKM, HI and NHI of the genotypes. The NUE components NupE%, NUEYld and NutYld were also reduced by the HN treatment.

Olifants, Kariega and Marico showed good responses in the agronomic components, with Inia, SST 806, SST 822, Olifants, Kariega and Marico having high values for NUE components. The cultivar Olifants had the highest Ngrain, Ntotal and NHI, although differences between parents were small. SST 806 had the highest BM, NupE%, NUEYld and NutEYld, and Olifants the highest values for AEGP and NPE. The F_2-offspring Olifants x Steenbras, SST 806 x SST 822, Marico x Steenbras, Olifants x SST 822 and Marico x SST 806 showed high responses in the measured agronomical and NUE components. SST 822 had a reduced total N uptake, also confirmed by reduced NUE components. Cultivars responded differently at the two N treatments in measured and calculated agronomic and NUE components.

The calculated correlation matrixes for the environments indicated positive coefficients for several of the agronomic and calculated components. Biomass and grain yield was highly correlated with the NUE components, NupE%, NUEYld, Ngrain and Ntotal at both environments. Grain protein was negatively correlated to NutEYld, while NHI was positively correlated to this component. This again points to the first order importance of grain yield production before grain protein under limiting N availability conditions. The correlation coefficients of components BM, grain yield, NPE, NRE and NUEYld increased at the HN treatment.

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CHAPTER 5

ASSESSMENT OF THE GENERAL AND SPECIFIC COMBINING ABILITIES AND HERITABILITIES FOR NITROGEN USE EFFICIENCY COMPONENTS IN SOUTH AFRICAN IRRIGATED WHEAT GENOTYPES

5.1 Introduction

Wheat (*Triticum aestivum* L.) grain yields have increased substantially since the 1950's. About half of this yield improvement has resulted from genetic increases in grain yield and the other half is due to improved production technologies and practices (Frederick & Bauer, 1999). Genetic improvement in wheat yield can be attributed to selection for improved agronomic characteristics conferring either higher yield potential or greater stress tolerance (Slafer *et al*., 1993). Processes identified as having a significant effect on wheat growth and development include nutrient uptake and metabolism, photosynthesis and respiration, carbon partitioning, leaf senescence, and plant water relations (Frederick & Bauer, 1999). It is generally believed that wheat grain yield is a function and integration of all these processes, each of which can be altered by the climatic conditions during the growing season and the cultural practices applied in crop production.

At the beginning of the century, when the important contribution of nitrogen (N) nutrition to grain yield became evident and the synthesis of ammonium from atmospheric N made fertilizers available on a large scale, it was found that available wheat varieties were not able to exploit the extra fertility induced by N fertilizer because of their intrinsic susceptibility to lodging (Borghi, 1999). Breeders were therefore stimulated to develop a new plant ideotype more tolerant to high N fertilization and subsequent increased lodging, which in time lead to the development of semi-dwarf high-input high-yielding varieties. However, the efficiency mechanisms of the plant also become important at very low levels of N availability when the yield level is below the economical threshold.

Higher yielding wheat cultivars are generally shorter, earlier maturing, often has more tiller/ears than older cultivars. Harvest index of mature crops is the ratio of economic product (grain) to the aboveground biomass at harvest (Snyder & Carlson, 1984). It estimates the partitioning of the dry matter between grain and the stems and leaves of the plant. The increased yield with modern cultivars is principally attributed to greater distribution of above ground biomass to the grain, i.e. a higher harvest index (HI). Harvest index is correlated positively with grain yield and negatively with biological yield.

The HI and grain growth rate is also higher in newer released wheat cultivars (Simmons, 1987). There are however, limits to the possible increases in HI and a value of 50-60 has been estimated. It has been shown that the increases in wheat yield from previous breeding were almost exclusively associated with parallel increases in HI (Slafer *et al.*, 1999). A decline in crop height associated with the yield improvement was also noted (Simmons, 1987), although plant height has a biological limit with the optimum height range of between 70 and 100 cm.

A recent review of N use efficiency (NUE) in cereal production identified world-wide efficiencies of only 33% for fertilizer N (Johnson & Raun, 2003). Crop requirement of N is directly related to potential yield and is supplied by fertilizer and non-fertilizer N. It is usually observed that after several decades of crop production in a system of conventional tillage, yield without fertilizer N will be relatively low and constant, consistent with the decreased level of organic N in these soils (Johnson & Raun, 2003). However, the response to application of fertilizer N is variable because of annual variability in yield potential due to climatic conditions, and the contribution to crop N requirement from non-fertilizer sources.

Wheat varieties with high HI values are known to have higher NUE values (Thomason *et al.*, 2002). It has also been reported that wheat varieties that accumulate large amounts of N early in the growing season do not necessarily have high NUE values. Plants must translocate this previously accumulated N to the grain and must assimilate additional N after anthesis to produce a high NUE (Cox *et al.*, 1985). Generally under field conditions, N in the grain is derived mainly from organic N present as components of vegetative plant parts that is remobilized during grain filling. Leaves may contribute 40%, non-grain spike tissues 23%, the stem 23%, and the roots 16% of the N being translocated to the grain during mid-grain filling (Simmons, 1987), depending on environmental conditions.

The extent of N remobilization in wheat has been expressed by means of the Nitrogen harvest index (NHI), which is defined as the proportion of total aboveground plant N present in the grain. The concentration of N remaining in a vegetative plant part at maturity may also be a good indicator of how extensively N was mobilized from that plant part (Simmons, 1987). Dry matter accumulation, synthesis, translocation, partitioning and accumulation of the photosynthetic products within the plant are controlled genetically, but can be significantly influenced by the environment (Snyder & Carlson, 1984). Since most variety selection is done under high N fertility conditions, efficiency of

N use is often considered second in importance to grain yield. This approach will have to change in response to the worldwide need for increasingly nutrient efficient crops (Thomason *et al*., 2002).

Growing environmental concerns and lower commodity prices tend to favor agricultural systems with lower input levels. Studies on genetic gain have shown that, though genetic progress exists at all input levels, genetic gain is lower under low input levels (Ortiz-Monasterio *et al*., 1997; Brancourt-Hulmel *et al*., 2005). This situation may have resulted from breeding that has been conducted under either high or low input fertilizer N levels. Genetic gain measured under low-input levels was then probably due to indirect selection. The relative gain of indirect versus direct selection, considering equal selection intensities, depends on heritabilities at both input levels and genetic correlation between input levels (Falconer, 1974). Selection in stress environments will favor selection of adaptation characteristics, while breeding in favorable environments will select for characters linked to maximum yield potential (Brancourt-Hulmel *et al*., 2005).

Genetic selection is often conducted with high fertilizer inputs to eliminate available N as a variable; however, this can mask efficiency differences among genotypes in accumulating and utilizing N to produce grain (Kamprath *et al*., 1982). This is also consistent with findings that high yielding varieties released during the Green Revolution were selected to respond to high N inputs (Earl & Ausubel, 1983). Consequently, continued efforts are needed to include plant selection under low N – something not often considered a priority by plant breeders, and uncharacteristic of most agricultural experiment stations (Raun & Johnson, 1999).

Plant genetic variability can be defined as the heritable character of a particular crop species or cultivar that shows differences in growth or production in comparison with other species, or cultivars of the same species, under favorable or unfavorable growth conditions (Fageria & Baligar, 2003). Comparative studies of wheat cultivars from different breeding eras revealed that modern cultivars often out-yield earlier released cultivars. However to obtain a simultaneous improvement in grain yield and grain protein percentage by breeding is considered challenging because of the negative relationship usually found between these traits (Slafer *et al*., 1993; Lawlor, 2002). Protein cannot form without N therefore an adequate supply of N is prerequisite for high protein yields.

Differences between species and genotypes in their ability to absorb, translocate, and utilize soil and fertilizer N can be ascribed to variations in plant growth rate and morphology, as well as the capacity for uptake and metabolism. High yielding cultivars are characterised by rapid growth rates resulting in high dry matter production per unit land area that must be met by an adequate supply of N (Bänziger *et al*., 1992). Genotypes also differ in their capacity to produce dry matter at a given level of N supply (Bänziger *et al*., 1992). They also vary in their capacity to absorb, translocate, and partition N within the plant. For grain crops this is important since remobilization of N from the tillers and leaves is an important source of grain N (Clark, 1983).

Field experiments have shown that genetic variability in N uptake exists in small grains (van Sanford & MacKown, 1986). Genotypic variation has also been reported for N utilization efficiency expressed as the ratio of grain yield to total plant N but variation in grain yield is rather explained by N uptake than N utilization (van Sanford & MacKown, 1987). Genotypic variability was found for N accumulation and/or remobilization. Therefore, a concomitant increase in grain yield and grain protein seems feasible (Bänziger *et al*., 1992). The environmental and genetic variation in grain protein concentration was described extensively by Kramer (1979) who also discussed breeding methods to alleviate the negative yield-protein content relationship.

The physical constraints imposed by soil on roots are substantially different from those imposed on the aboveground fraction of the plant. Measurements of root distribution of growing plants as a function of distance from the surface shows a pattern that is simply described as a logarithmic decrease in root density with distance from the soil surface, with this logarithmic distribution moving downwards as the plant grows (Andrew, 1987). The root distribution of a plant is primarily governed by its genome, which determines the morphology of its root system (Andrén *et al*., 1991). Within the genetic restraints, root distribution is also governed by availability of nutrients and soil water content as well as the penetration resistance of the soil (Scott-Russell, 1977). In general, roots grow rapidly in those areas of the soil rich in needed nutrients and resources, which thus become efficiently exploited over time. Therefore, it can be assumed that root density will be positively correlated with the availability of limited resources. As the root system grows and increasingly exploits the needed resource, the initial positive correlation should weaken and may even become negative (Drew, 1975).

The differential response of cultivars to N management could also be linked to their specific N requirements at certain stages of plant development during the growing season. Sufficient N is supplied to the grains through a greater remobilisation of nitrogenous compounds from the vegetative organs to the grains or by means of a greater uptake by the root system. It is postulated that the above-mentioned process could be supported by genetic means, thereby increasing the proportion of plant nitrogen that is deposited in the grain as protein. The N harvest index (NHI = proportion of seed N to total biomass N) is considered a measure of how efficiently a plant utilizes acquired N for the production of grain protein. Depending on climate, cereal species, cultivar and management techniques, 40-90% of total biomass N is stored in the grains. This suggests that it is unlikely that grain protein yield can be increased by genetically improving partitioning efficiency (Feil, 1997).

Another possibility for enhancing the amount of N in the plant is to breed for higher N uptake or to reduce the loss of N from the plant. Estimation of genetic variance components is an important part of quantitive genetics. A generic mating design is often required to reach this goal, including the various types of diallel mating designs (Griffing's mating designs). Usually, the ANOVA approach is used to estimate these genetic variance components (Wu *et al.*, 2006). Optimum allocation of resources in hybrid breeding depends on efficient methods for choosing parents and identifying superior hybrid combinations. Griffing (1956) described two main models and four different methods for the diallel analysis of data. For the purpose of this study Model 1, Method 2 was used. Model 1 implies that the experimental material is to be regarded as the population about which conclusions are to be made. Method 2 implies a half diallel, where only the parents and one set on F_1-hybrids are included. With Method 2 the reciprocal crosses are not included in the analysis.

Combining ability has been defined as the performance of a line in hybrid combinations (Kambal & Webster, 1965). Assessment of the combining ability could be useful to define the contribution of a variety to the performance of it's progeny, because it defines the ease with which progress through selection can be made.

Gene action is divided into two categories (Sprague & Tatum, 1942; Rojas & Sprague, 1952) namely general combining ability (GCA) and specific combining ability (SCA). They defined GCA as the average performance of lines in a number of hybrid combinations and that of SCA as deviations of certain crosses from expectations based on the average performance of lines involved. The analysis of combining ability provided information about the relative importance of the general (GCA) versus specific combining abilities (SCA) effects and gave an indication of the gene action involved in the inheritance of the traits (Oettler *et al.*, 2005). Additive and dominance genetic effects were also calculated. The GCA effects aim to identify the best combiners under low and high N availability conditions. The SCA effects calculated for the hybrids aim to identify the best specific hybrid combinations for the various components under the respective N conditions. Two tailed *t*-tests were used to test for significant differences between GCA and SCA effects where $t=GCA/SE_{GCA}$ or SCA/SE_{SCA} respectively (Cox *et al*., 1985; Roy, 2000).

General combining ability is largely due to additive gene effects and higher order additive gene interactions. The SCA effect is largely a function of non-additive dominance gene effects and other types of epistasis (inter-allelic gene interactions) as well as genotype x environment interaction (intra-allelic interaction) (Griffing, 1956; Cukadar-Olmedo *et al*., 1997). Thus, significant values of SCA could be interpreted as indications of the predominance of non-additive gene effects caused by dominance and epistasis (Kambal & Webster, 1965). The ratio of GCA:SCA can reveal the nature of genetic variance. Should the GCA variance be greater than SCA variance, a higher ratio is eminent indicating the prevalence of the additive genes versus the non-additive components (Sayed, 1978). Significant additive genetic action for total N at maturity, biological yield and protein per kernel was also calculated by Koekemoer (1996) for tested South African irrigated wheat cultivars.

Mihaljev & Kovacev-Djolai (1978) found highly significant SCA and GCA values in a study on combining ability of wheat for grain protein content, and postulated that improvement in F_1-hybrids could be achieved by selective choice of parents carrying the dominant gene for high grain protein content. Koekemoer (1996) found in his study that the parents tested (irrigated South African wheat cultivars) differed in biomass, grain protein yield and grain yield. He also found significant phenotypic correlations between total N at maturity and grain yield (0.65), and between grain yield and grain protein yield. He also found differences in GCA values for biological yield, grain protein, and other N related characteristics, and identified several specific hybrid combinations.

Heritability is a measure of the correspondence between breeding values and phenotypic values (Jones, 1986; Falconer & Mackay, 1996). Allard (1960) used the term heritability to specify the genetic portion of the total variability. Successful selection is dependent on a high heritability of characteristics. Heritability can be expressed in a broad-sense or narrow-sense (Roy, 2000). Broad-sense heritability (h^2_b) is the ratio of the genotypic variance including additive dominance and epistatic variance to the phenotypic variance ($\sigma^2_g/\sigma^2_{ph}=\sigma^2_g/(\sigma^2_g+\sigma^2_e+\sigma^2_{ge})$), it expresses the extent to which individuals' phenotypes are determined by the genotypes. Narrow-sense heritability is a ratio of the additive genetic variance to the phenotypic variance (σ^2_A/σ^2_{ph}), it expresses the extent to which phenotypes are determined by the genes transmitted from the parents (Roy, 2000). Heritability in the narrow-sense determines the degree of resemblance between relatives (Falconer & Mackay, 1996), and measures the relative importance of additive portion of the genetic variance that can be transmitted to the next generation of offspring. Therefore, it is of great importance in breeding programmes to predict the expected gain from selection for a character (Fehr, 1987; Falconer & Mackay, 1996).

McKendry *et al*. (1988) concluded that all the NUE characteristics studied in their research were under genetic control, with additive gene action being significant for the characteristics. Dominant gene action was detected for these characteristics but the degree and direction was both trait and genotype specific. The studied characteristics were grain protein concentration, grain protein yield, total N at maturity, NHI, grain yield and harvest index. Variance analysis indicated a large genetic component of the variation relative to the environmental component for all the characteristics studied.

Heritability is not a constant value since decisions by the breeder can influence the magnitude of the value and the amount of genetic improvement obtained from selection. Heritability estimates provide an indication of the expected response to selection in segregating populations, and in theory, both h^2_b and h^2_n can vary from 0 to 1. A high estimate indicate how well evaluation of the parents will predict what the progenies will be like with a particular combination of breeding material and technique of evaluation (Jones, 1986). Characteristics with high h^2_n values can be improved more rapidly with less intensive evaluation than those with low values and hence h^2_n is useful in calculating selection progress estimates. The h^2_b overestimates the response to selection as it includes non-additive effects (Dudley & Moll, 1969).

The successful commercial production of available wheat cultivars thus depends on sound N fertilization guidelines in general. However, specific cultivar responses to N management and therefore N requirements vary according to growth patterns and yield potential development. Management aimed at achieving high yields with acceptable grain quality must therefore be adapted to the specific cultivar.

The potential for breeding for NUE in crops is dependent on the genetic variability resent in the species for the trait(s) that determine efficient N utilization, and the development of procedures to accurately measure components that reflect N use by the plant (Sherrard *et al*., 1984). Genetic variability for NUE has been reported (Ortiz-Monasterio *et al*., 1997). In the semi-dwarf cultivars originating from CIMMYT the increase in grain yield has been associated with gains in both NUE components: uptake and utilization efficiency at the medium to high levels of N fertility, and only with uptake efficiency under low N fertility. This suggests that the level of N in the soil plays a very important role in the genetic expression of uptake and utilization efficiency in wheat (Ortiz-Monasterio *et al*., 1997). Wheat grain protein was shown to be genetically controlled and significant genotypic or varietal differences in this characteristic have been noted. It was also found that grain protein is strongly affected by environmental factors and agricultural practices like N fertilization and soil water management (Mihaljev & Kovacev-Djolai, 1978). The use of diallel analysis lends itself to detailed genetic analysis, and it can provide insight into the nature of genetic variances and the magnitude of is components (Sayed, 1978).

The traditional objectives of the wheat breeder are to develop cultivars with a stable and high yield and good grain quality characteristics. For the effective improvement of quality and yields, a plant breeder must have knowledge of the inheritance of quality traits and the joint inheritance of quality and agronomic characteristics (Baker *et al*., 1971). The use of more N efficient cultivars can either reduce N applications or reduce the environmental risk related to high N use in agriculture. The efficient use of N in the soil-plant system can also result in cultivars producing high yields with high grain protein.

There is limited information available on the N use efficiency components of wheat cultivars currently cultivated under irrigation. It is therefore evident that as N is an important plant nutrient, studies aimed at improving NUE and related crop responses should assess the grain yield, the N uptake and N use efficiency of selected irrigated wheat cultivars and F_2-offspring by comparing the different measured agronomic and physiological N use efficiency components. The aim of this study was to;

- Determine the GCA and SCA effects of irrigated cultivars for the NUE components;
- To calculate GCA:SCA ratios to indicate additive or non-additive gene action;
- To calculate broad- and narrow-sense heritability estimates.

5.2 Material and Methods

5.2.1 Parental cultivars

The following seven commercially available spring wheat cultivars were randomly chosen for this study: Kariega, Marico, Olifants, Steenbras, SST 806, SST 822 and Inia.

Selected agronomic characteristics of these cultivars are as follows:

Kariega – High yielding cultivar with good grain quality characteristics and wide adaptability.
Marico – Medium to high yielding cultivar.
Olifants – High yielding cultivar with good grain quality characteristics, and is widely adapted.
Steenbras – Low to medium yielding cultivar, suitable for later planting dates.
SST 806 – High yielding cultivar with reduced lodging susceptibility.
SST 822 – Medium yielding cultivar with double dwarf genes, and is adapted to later planting dates.
Inia – Low to medium yielding cultivar that is adapted to a range of planting dates.

5.2.2 Development of F_2-hybrids

The selected parental cultivars were planted in pots in the greenhouse at the Small Grain Institute near Bethlehem from May to June 2002. It was planted at two-weekly intervals to synchronize pollen availability for cross-fertilization. Applicable fertilization, disease and insect control practices were followed to ensure optimal growth and development of plants. The parents were crossed in a half-diallel according to Griffings' model 1 method 2 (Griffing, 1956). A half-diallel design was used because reciprocal differences are not significant in wheat (Joshi *et al.*, 2004).

The methodology for the crossing of self fertilized crops according to Allen (1980) was used to generate 21 F_1-hybrid combinations. The F_1-hybrid seeds of each cross were harvested separately and multiplied in the greenhouse during 2003. The experimental material for this study consisted of seven parental cultivars and their 21 F_2-offspring and is shown in Table 5.1. The F_2-seeds generated from the F_1-plants provided sufficient seeds to plant two different localities with two N application treatments at each locality. Paroda & Joshi (1970) studied the combining ability for grain yield and yield components in wheat using F_2-generation data. Although results were similar to those obtained from earlier F_1 data, the F_2-generation showed a decline in the estimate of SCA variance, attributed to the reduction of dominance from F_1- to F_2-generations. The F_2-generation however, can effectively be used for the identification of significant GCA effects.

Table 5.1 Seven parental cultivars and their F_2-offspring tested in field trials at Bethlehem and Vaalharts during 2004

Entry	Parents	F_2-offspring
1.	Kariega	
2.	Marico	
3.	Olifants	
4.	Steenbras	
5.	SST 806	
6.	SST 822	
7.	Inia	
8.		Kariega x Marico
9.		Kariega x Olifants
10.		Kariega x Steenbras
11.		Kariega x SST 806
12.		Kariega x SST 822
13.		Kariega x Inia
14.		Marico x Olifants
15.		Marico x Steenbras
16.		Marico x SST 806
17.		Marico x SST 822
18.		Marico x Inia
19.		Olifants x Steenbras
20.		Olifants x SST 806
21.		Olifants x SST 822
22.		Olifants x Inia
23.		Steenbras x SST 806
24.		Steenbras x SST 822
25.		Steenbras x Inia
26.		SST 806 x SST 822
27.		SST 806 x Inia
28.		SST 822 x Inia

5.2.3 Environments

Two irrigated environments (namely Vaalharts and Bethlehem) were selected to test the experimental material. The detail of the environments, soil profile descriptions and soil analysis results for the 2004-growing season, were discussed in Chapter 4.2.3 and 4.7.

5.3 Experimental layout and treatments

A randomized split plot design was used with parents and F_2-offspring as sub treatments and the N treatments as main plots. Three replicates of each entry x treatment combination were planted.

5.3.1 Nitrogen treatments

Two N treatments were tested:

- **Low Nitrogen treatment - LN** - an N omission scenario where only phosphorus (50 kg P/ha) and potassium (20 kg K/ha) were applied.
- **High Nitrogen treatment - HN -** an optimally N managed scenario tested that received similar phosphorus and potassium applications and a recommended rate of N (180 kg N/ha) applied during the growing season at planting (120 kg N/ha), and at stem elongation (60 kg N/ha).

5.3.2 Planting of experimental material in 2004

Each plot consisted of six 1.5 m rows with an interrow spacing of 17 cm. Seed of the respective parents and offspring were space-planted (5 cm interplant spacing). The trial at Bethlehem was planted on 8th of July and Vaalharts on 20th of July respectively. The preceding crop planted at Vaalharts was maize (2003/4), while at Bethlehem the previous crop was dryland wheat (2003) in a monoculture cropping system using conventional cultivation practices. Conventional soil cultivation practices were followed after harvest and during the fallow period succeeding the previous crop, which included discing, ploughing and seedbed preparation. Border plots were planted between the N treatments and around the trials to limit external competition.

5.3.3 Fertilization

Phosphorus and potassium applications were based on the soil analysis values of the trial sites before planting in 2004. The fertilizer requirement was broadcasted and incorporated during final seedbed preparation before the planting of the respective trials. The N treatment applications were applied to the specified treatment plots at planting.

5.3.4 Other management factors

Light irrigations were applied after planting to initiate germination and aid seedling emergence. Irrigation scheduling from emergence onwards was managed with relevant crop growth factors linked to daily evaporation pan measurements from weather stations in the vicinity of the trial sites, and overhead sprinkler systems were used to replenish the calculated soil water deficit. Crop growth was monitored during the growing season to eliminate non-treatment nutritional deficiencies, apply weed, disease and insect control when necessary to ensure optimal growth.

5.4 Characteristics measured

Measurements and calculated components are based on studies by Moll *et al*. (1982), Doyle & Holford (1993), Ortiz-Monasterio *et al*. (1997) and Fageria & Baligar (2003). The measurement and calculation details of the agronomical characteristics, calculated N uptake components and NUE components were discussed in Chapter 4.4.

5.5 Statistical analyses

5.5.1 Combined analysis of variance (ANOVA)

The combined dataset (Genotypes X Environments x N treatments) for 2004 were analyzed with Gen Stat 8 (Genstats 8th edition, 2006, Lawes Agricultural Trust) following applicable procedures for analyses of split plot experimental designs. The N treatments were analyzed as main plots, with the genotypes tested as subplots. Analysis of variance was done for each of the measured characteristics and calculated components.

The ANOVA is used to evaluate the responses of each genotype for each characteristic within each experiment (Ehdaie *et al*., 1988). Significant differences between genotypes identified by the ANOVA allowed for the analysis of combining abilities to proceed. The diallel analysis of Griffing (1956) was used to calculate the general combining abilities (GCA) and the specific combining abilities (SCA). Data was analysed according to model 1, method 2. The N treatments were analyzed individually per environment, and the estimates of GCA and SCA of the parents were calculated via Agrobase 21 (Agronomix Software Inc., 2000). The GCA:SCA ratio's and heritabilities were also calculated. The least significant differences (LSD) were calculated with the Student *t*-test at a 95% confidence level (Roy, 2000).

5.6 Results and discussion

5.6.1 Analysis of variance (ANOVA) for General Combing Ability (GCA) and Specific Combing Ability (SCA) for tested wheat genotypes at Bethlehem

5.6.1.1 Agronomic characteristics

The ANOVA tables for the measured agronomic characteristics are presented in Table 5.2. The hybrid effect was significant for the biomass (BM) measured at both the LN and HN treatments. However, the GCA effect was not significant at the LN treatment, but significant at the HN treatment, with SCA effects significant at both N treatments. The SCA effect indicated significant genetic variability at both N treatments.

The analysis of grain yield (Yld) showed a significant response with the hybrids tested, but only the SCA effect was significant at both N treatments. This indicates specific combinations to be significantly better at the tested N treatments. The GCA effect was not influenced by N application and was not significant at both LN and HN treatments. The analysis of hectolitre mass (HM) showed that neither the hybrid, nor the GCA and SCA effects were significant at the LN treatment, but significant at the HN treatment. The significance of the combining abilities can therefore only be assessed at optimum nitrogen levels.

For thousand kernel mass (TKM) only GCA was significant at both the LN and HN treatments, with SCA non-significant for this component. This indicates that the combinations for this measured component can be tested at both high and low N availability levels. A similar response pattern was found for grain protein (GP), with only GCA being significant. The GCA of the respective parents can therefore be expressed at both levels of N application. Although the hybrid effect for harvest index (HI) was significant, only the GCA effect at the HN treatment was significant. This indicates that although there were significant responses in BM and yield with regards to GCA and SCA effects, the different N levels had no significant affect on the HI.

5.6.1.2 Calculated Nitrogen uptake components

The ANOVA tables for the calculated N uptake components are presented in Table 5.3. The analysis of N uptake in the grain (Ngrain) showed that the hybrid and GCA effects were significant at the HN treatment. The SCA for Ngrain was significant at both the N treatments. Certain combinations of the hybrids showed positive Ngrain responses at the LN treatment, while the GCA and SCA effects were more pronounced at the HN treatment. This is probably due to the effect of certain dominant genes or interaction between genes. A similar response pattern was found for total N uptake (Ntotal). This

Table 5.2 Analysis of variance (ANOVA) for combining abilities (GCA and SCA) for measured agronomic characteristics of wheat genotypes planted at Bethlehem in 2004

		BM[a]		Yld[b]		HM[c]		TKM[d]		GP[e]		HI[f]	
Source of variation	**df**	**LN**	**HN**	**LN**	**HN**	**LN**	**HN**	**LN**	**HN**	**LN**	**HN**	**LN**	**HN**
Replicates	2	45956.041	255518.824	0.92735082	2.92674033	24.895714	1.95583333	82.6353571	11.32	7.09840833	0.13388929	0.02371205	0.00331433
Hybrids	27	56025.445*	78281.291**	1.31869972**	1.96138134**	2.902892	7.429647**	22.4163**	18.2703941**	0.52836966*	0.5857986**	0.00678247*	0.00446654*
GCA	6	60189.833	88608.999*	0.34524949	1.48262296	2.542522	12.0390653**	69.9851675**	35.2957319**	0.83678448*	1.75386226**	0.0061865	0.00624666*
SCA	21	57452.828*	61145.741*	1.56773778**	2.08306401**	3.086065	6.9234977**	8.7977176	14.6380185	0.45841037	0.30773516	0.00626784	0.00400255
Error	54	29498.826	24299.455	0.53345639	0.7594632	1.841887	2.8427469	7.370172	8.4503704	0.28148117	0.24807324	0.00371531	0.00237517

[a] BM: Biomass; [b] Yld: Grain yield; [c] HM: Hectoliter mass; [d] TKM: Thousand kernel mass; [e] GP: Grain protein percentage; [f] HI: Harvest index.

P < 0.001	**
P < 0.001 - 0.05	*

indicate that it is possible to improve N uptake components effectively at the HN treatment.

Table 5.3 Analysis of variance (ANOVA) for combining abilities (GCA and SCA) for calculated N uptake components of wheat genotypes planted at Bethlehem in 2004

		Ngrain[a]		Ntotal[b]		NHI[c]	
Source of variation	**df**	**LN**	**HN**	**LN**	**HN**	**LN**	**HN**
Replicates	2	1306.55144	1344.1183	1484.19059	4553.72263	0.0044105	0.01075751
Hybrids	27	495.99992*	1037.14603*	591.26713*	1493.7575**	0.0046509	0.00484696**
GCA	6	103.7601	882.17502*	269.05876	1480.06106*	0.0040116	0.00944539**
SCA	21	592.12784**	1086.43761*	683.29083*	1263.02986**	0.0044632	0.00284269
Error	54	218.3176	364.35996	310.57918	481.02787	0.00279	0.00189757

[a]Ngrain: Nitrogen uptake in the grain; [b]Ntotal: Total Nitrogen uptake; [c]NHI: Nitrogen harvest index.

P < 0.001 **
P < 0.001 - 0.05 *

The analysis of N harvest index (NHI) however, showed that the hybrid and GCA effects were significant only at the HN treatment. This indicates the positive effect of N application on N uptake in general, but also on the partitioning of N to the grain. In this specific cropping environment the general combining abilities of the parents for NHI were expressed at the high N treatment.

5.6.1.3 Calculated NUE components

The ANOVA tables for the calculated N use efficiency components are presented in Tables 5.4 and 5.5.

Table 5.4 Analysis of variance (ANOVA) for combining abilities (GCA and SCA) for NUE components of wheat genotypes planted at Bethlehem in 2004

		NupE%[a]		NUEYld[b]		NutEYld[c]	
Source of variation	**df**	**LN**	**HN**	**LN**	**HN**	**LN**	**HN**
Replicates	2	1058.88702	511.454449	66.196237	32.86607337	41.994294	12.17619037
Hybrids	27	421.84036*	167.769738**	94.090164*	22.0297663**	21.925641	11.0548251*
GCA	6	191.964046	166.229942**	24.637043	16.6572539	28.906221	19.7926973**
SCA	21	487.493008	141.855518**	111.860468**	23.3957058**	20.023466	8.5562615
Error	54	221.58516	54.025737	38.057149	8.5298569	13.985438	6.0028234

[a]NupE%: Nitrogen uptake efficiency; [b]NUEYld; Nitrogen use efficiency for grain yield; [c]NutEYld: Nitrogen utilization efficiency for grain yield.

P < 0.001 **
P < 0.001 - 0.05 *

The N uptake efficiency (NupE%) only showed significant GCA and SCA effects at the HN treatment. Under limiting N availability conditions (the LN treatment) the expression of variability in N uptake ability is suppressed. With regards to the NUE for grain yield (NUEYld), the SCA effects were significant at both LN and HN treatments. The pattern changed with the analysis of N utilization efficiency for grain yield (NutEYld), with only the GCA effect at the HN treatment being significant. This points to certain parents that were better general combiners for NutEYld.

Table 5.5 Analysis of variance (ANOVA) for combining abilities (GCA and SCA) for calculated NUE components of wheat genotypes planted at Bethlehem in 2004

Source of variation	df	AEGP[a]	NAEYld[b]	NPE[c]	NRE[d]
Replicates	2	0.00001	10.151	0.44	97.246
Hybrids	27	0.0001**	121.258**	427.837**	561.15**
GCA	6	0.0001*	12.663ns	107.642**	144.16*
SCA	21	0.0001**	48.35**	152.604**	199.304**
Error	54	0.0001	22.842	10.707	56.312

[a]AEGP:Agronomic efficiency for grain protein; [b]NAEYld: Agronomic efficiency for grain yield; [c]NPE:Physiological efficiency; [d]NRE: Recovery efficiency.

P < 0.001	**
P < 0.001 - 0.05	*

The ANOVA results for agronomic efficiency for grain protein (AEGP), physiological efficiency (NPE) and apparent recovery percentage (NRE) show that the hybrid, GCA and SCA effects were significant for these calculated components (Table 5.5), with the exception of the GCA effect for agronomic efficiency for grain yield (NAEYld).

5.6.2 Analysis of variance (ANOVA) for General Combing Ability (GCA) and Specific Combing Ability (SCA) for tested wheat genotypes at Vaalharts

5.6.2.1 Agronomic characteristics

The ANOVA results for the measured agronomic characteristics are presented in Table 5.6. The analysis of the BM showed that the hybrid, GCA and SCA effects were significant at both LN and HN treatments. A similar response was found for grain yield.

The analysis of HM showed that only the GCA effects at the LN and HN treatments were significant. The TKM values showed the same response pattern, with only GCA being significant. Grain protein (GP) showed no significance in calculated means square errors for the hybrid, GCA, and SCA effects.

The analysis of HI showed that the hybrid and GCA effects were significant at both N treatments, but SCA was non-significant. Therefore, there are parents that induce changes in HI when used in hybrid combinations, probably due to specific gene combinations.

Table 5.6 Analysis of variance (ANOVA) for combining abilities (GCA and SCA) for measured agronomic characteristics for wheat genotypes planted at Vaalharts in 2004

		BM[a]		Yld[b]		HM[c]		TKM[d]		GP[e]		HI[f]	
Source of variation	**df**	**LN**	**HN**	**LN**	**HN**	**LN**	**HN**	**LN**	**HN**	**LN**	**HN**	**LN**	**HN**
Replicates	2	2025.1902	76758.2741	0.02956844	1.01112525	1.97011905	3.90154762	2.0633333	27.3433333	0.07260833	0.78640119	0.00325565	0.00039015
Hybrids	27	29035.2514**	118086.008**	0.37397035**	1.6340959**	5.1865271	3.5103038	15.943202	13.0424138**	0.17764245	0.46685603	0.00867749*	0.00446074*
GCA	6	39742.4298**	187672.553**	0.53151284**	3.78861095**	15.88848325**	7.88934744**	44.9129453**	36.4058025**	0.09471287	0.47021905	0.02098547**	0.01012336**
SCA	20	29785.405**	99703.706**	0.36836068**	1.08090242**	2.55338657	2.33223148	9.2610926	5.2220926	0.19229664	0.42066021	0.00576736	0.00338551
Error	54	10730.1094	37880.422	0.12147927	0.27090305	3.5169092	2.4115476	10.2193827	5.1571605	0.18868981	0.30243576	0.00429758	0.00219657

[a] BM: Biomass; [b] Yld: Grain yield; [c] HM: Hectoliter mass; [d] TKM: Thousand kernel mass; [e] GP: Grain protein percentage; [f] HI: Harvest index.

P < 0.001 **
P < 0.001 - 0.05 *

5.6.2.2 Calculated Nitrogen uptake components

The calculated N uptake components are shown in Table 5.7. The mean square errors of hybrids, GCA and SCA for Ngrain and Ntotal indicate significance for both N treatments. The analysis of NHI indicated that the hybrid, GCA and SCA effects were significant at the HN treatment. This is a result of the positive effect of N application on Ngrain and Ntotal.

Table 5.7 Analysis of variance (ANOVA) for combining abilities (GCA and SCA) for calculated N uptake components of wheat genotypes planted at Vaalharts in 2004

		Ngrain[a]		Ntotal[b]		NHI[c]	
Source of variation	**df**	**LN**	**HN**	**LN**	**HN**	**LN**	**HN**
Replicates	2	6.114149	477.524407	15.8752947	1026.611604	0.00202751	0.00065433
Hybrids	27	119.775712**	749.42271**	186.940787**	1006.7495**	0.00233077	0.01050824**
GCA	6	181.895888**	1807.93362**	246.091124**	1497.89813**	0.00217494	0.03019706**
SCA	21	116.227913**	461.93096**	193.431658**	801.12927**	0.00246131	0.0060486*
Error	54	39.226206	137.59526	62.683389	279.99112	0.00207023	0.00270464

[a]Ngrain: Nitrogen uptake in the grain; [b]Ntotal: Total Nitrogen uptake; [c]NHI: Nitrogen harvest index.

P < 0.001 **
P < 0.001 - 0.05 *

5.6.2.3 Calculated NUE components

The ANOVA results for the N use efficiency components are shown in Table 5.8 and 5.9. All the calculated effects were significant at both N treatments for both NupE% and NUEYld. However, for NutEYld only the hybrid and GCA effects at the HN treatments were significant. The positive effect of N application aided the expression of the parents used in the hybrid combinations. The non-significant effects at the LN treatment indicate that in a restricted N availability environment, the responses in grain yield produced to N taken up by the plant were restricted as well.

Table 5.8 Analysis of variance (ANOVA) for combining abilities (GCA and SCA) for NUE components of wheat genotypes planted at Vaalharts in 2004

		NupE%[a]		NUEYld[b]		NutEYld[c]	
Source of variation	**df**	**LN**	**HN**	**LN**	**HN**	**LN**	**HN**
Replicates	2	25.7849403	153.6772436	4.7994502	15.12491	11.25650565	0.8968866
Hybrids	27	303.675725**	150.706047**	60.760005**	24.4586689**	11.25891	23.1881266**
GCA	6	399.761174**	224.228293**	86.354731**	56.7096816**	6.6478313	55.4624502**
SCA	21	314.220049**	119.925002**	59.846888**	16.1786187**	11.8526439	16.1277992
Error	54	101.82868	41.913341	19.732431	4.054276	10.9046789	9.2098077

[a]NupE%: Nitrogen uptake efficiency; [b]NUEYld; Nitrogen use efficiency for grain yield; [c]NutEYld: Nitrogen utilization efficiency for grain yield.

P < 0.001 **
P < 0.001 - 0.05 *

The ANOVA results for NAEYld, NPE and NRE show that the hybrid, GCA and SCA effects were significant for these calculated components (Table 5.9), with the exception of the GCA and SCA effects for AEGP that were non-significant.

Table 5.9 Analysis of variance (ANOVA) for combining abilities (GCA and SCA) for calculated NUE components of wheat genotypes planted at Vaalharts in 2004

Source of variation	df	AEGP[a]	NAEYld[b]	NPE[c]	NRE[d]
Replicates	2	0.0400	7.521	50.189	24.891
Hybrids	27	0.000**	57.976**	163.157**	333.771**
GCA	6	0.000ns	45.47**	140.877**	177.194**
SCA	20	0.000ns	11.855**	29.674**	92.418**
Error	54	0.0000	9.679	25.795	85.031

[a] AEGP:Agronomic efficiency for grain protein; [b] NAEYld: Agronomic efficiency for grain yield; [c] NPE:Physiological efficiency; [d] NRE: Recovery efficiency.

P < 0.001 **
P < 0.001 - 0.05 *

5.6.3 General Combing Ability (GCA) effects for wheat genotypes at Bethlehem

5.6.3.1 Agronomic characteristics

The results as analysed for the GCA effects for the measured agronomic characteristics are presented in Table 5.10. The LN treatment had no significant effect on the calculated GCA effects of the parents for BM. At the HN treatment, Kariega was the parent with the highest GCA effect, but only Steenbras, SST 822, and Inia had significantly lower and negative GCA values.

The calculated GCA values for grain yield at both N treatments were not significantly different. This is in contrast to Paroda *et al*. (1970) that indicated significant GCA values for grain yield, and that this characteristic is controlled mainly through additive gene action. This lack of significance can in part be attributed to the possibility that a yield limit has been reached in the hybrids tested, or that the hybrids tested at Bethlehem were not adapted to the environment and showed no significant yield effects at the N treatments.

The GCA effects at the LN treatment of HM were not significantly different. At the HN treatment, Marico had the highest GCA value, with Kariega, Olifants, SST 806, and SST 822 with negative and significantly lower values. This is in part due to the negative response measured in HM with application of N. A similar pattern was observed for TKM, where values decreased at the HN treatment. At the LN treatment, Kariega had the highest GCA value, not differing significantly from SST 822 and Inia. At the HN treatment, Inia and SST 822 had the highest values, with Olifants at the lowest value.

Table 5.10 General combining ability (GCA) effects for agronomic characteristics of wheat genotypes at two N treatments planted at Bethlehem in 2004

Parents	BM[a]		Yld[b]		HM[c]		TKM[d]		GP[e]		HI[f]	
	LN	**HN**	**LN**	**HN**	**LN**	**HN**	**LN**	**HN**	**LN**	**HN**	**LN**	**HN**
Kariega	-42.632	58.812	0.022	0.027	0.077	-0.837	1.654	-0.419	-0.290	-0.241	0.019	-0.0193
Marico	68.379	41.895	0.179	0.198	0.137	0.856	-1.813	0.003	-0.115	-0.202	-0.011	-0.0001
Olifants	26.433	57.757	0.018	0.277	-0.415	-0.699	-2.498	-1.360	-0.067	0.374	-0.007	0.0002
Steenbras	43.322	-24.578	-0.011	-0.346	0.562	0.523	0.195	-0.501	0.224	0.135	-0.021	-0.0205
SST 806	-8.977	5.524	0.066	0.159	-0.063	-0.137	0.039	-0.293	-0.007	-0.303	0.015	0.0086
SST 822	-58.803	-49.846	-0.105	-0.065	-0.189	-0.311	1.610	0.240	0.152	0.197	0.012	0.0198
Inia	-27.723	-89.564	-0.169	-0.252	-0.108	0.604	0.813	2.329	0.103	0.040	-0.006	0.0113
LSD (0.05)	ns	83.323	ns	ns	ns	0.901	1.451	1.554	0.284	0.266	ns	0.0261

[a] BM: Biomass; [b] Yld: Grain yield; [c] HM: Hectoliter mass; [d] TKM: Thousand kernel mass; [e] GP: Grain protein percentage; [f] HI: Harvest index.

Jain & Singh (1970) and Singh *et al*., (1986) showed significant GCA effects for TKM in their results.

Steenbras had the highest GCA value for GP at the LN treatment, with only SST 806, Kariega and Marico at significantly lower values. Olifants was the best parent for GP at the HN treatment, with Kariega, Marico, SST 806 and Inia at significantly lower values. Mihaljev & Kovacev-Djolai (1978) also showed significant GCA effects for grain protein content in their studies. The GCA effects for HI was only significantly different at the HN treatment, and SST 822 was the best parent at the HN treatment, with Kariega, Marico and Steenbras at significantly lower GCA values. It is therefore possible to increase HI by selecting at the HN treatment.

5.6.3.2 Calculated Nitrogen uptake components

The analysis results for the GCA effects for the calculated N uptake components are presented in Table 5.11. The calculated GCA effects for Ngrain showed significant variability at the HN treatment. Olifants was the parent with the highest GCA value, with Kariega, Steenbras and Inia at significantly lower values. This response was also found in Ntotal with Olifants at the highest value, with Steenbras, SST 806, and Inia significantly lower. The GCA for NHI showed Inia at the highest value, with only Steenbras and Marico at significantly lower values.

Table 5.11 General combining ability (GCA) effects for N uptake components of wheat genotypes at two N treatments planted at Bethlehem in 2004

Parents	Ngrain[a]		Ntotal[b]		NHI[c]	
	LN	HN	LN	HN	LN	HN
Kariega	-1.7814	-1.9124	-3.7523	4.8143	0.0167	-0.0311
Marico	2.8520	2.5234	4.7160	4.6955	-0.0129	-0.0079
Olifants	-0.3345	10.4208	-0.0969	10.7319	-0.0010	0.0114
Steenbras	1.1817	-6.7576	3.4603	-5.9922	-0.0156	-0.0152
SST 806	1.5292	0.7629	0.2749	-2.8589	0.0113	0.0180
SST 822	-0.7329	0.5218	-1.6594	-0.2387	0.0069	0.0059
Inia	-2.7141	-5.5589	-2.9425	-11.1519	-0.0054	0.0188
LSD (0.05)	ns	10.203	ns	11.723	ns	0.0233

[a]Ngrain: Nitrogen uptake in the grain; [b]Ntotal: Total Nitrogen uptake; [c]NHI: Nitrogen harvest index.

5.6.3.3 Calculated NUE components

The analysis for the GCA effects for the calculated NUE components are presented in Tables 5.12 and 5.13. The calculated GCA value for NupE% at the HN treatment showed significant variability, with Olifants at the highest value, and Steenbras, SST 806 and Inia significantly lower.

A similar response was found in NUE for grain yield with significant variation found at the HN treatment. The NutEYld at the HN treatment showed that SST 806 had the highest GCA value, not significantly different from Inia, and with the other parents at lower values.

Table 5.12 General combining ability (GCA) effects for NUE components of wheat genotypes at two N treatments planted at Bethlehem in 2004

Parents	NupE%[a]		NUEYld[b]		NutEYld[c]	
	LN	HN	LN	HN	LN	HN
Kariega	-3.1693	1.6134	0.1830	0.0917	1.8510	-0.7285
Marico	3.9834	1.5736	1.5108	0.6653	-0.2088	0.1650
Olifants	-0.0819	3.5966	0.1544	0.9301	0.1775	-0.3928
Steenbras	2.9229	-2.0081	-0.0940	-1.1583	-1.4679	-0.9568
SST 806	0.2321	-0.9580	0.5561	0.5334	0.5335	1.4971
SST 822	-1.4016	-0.0800	-0.8828	-0.2186	-0.2292	-0.2626
Inia	-2.4855	-3.7374	-1.4275	-0.8435	-0.6561	0.6785
LSD (0.05)	ns	3.9289	ns	1.5611	ns	1.3096

[a]NupE%: Nitrogen uptake efficiency; [b]NUEYld; Nitrogen use efficiency for grain yield; [c]NutEYld: Nitrogen utilization efficiency for grain yield.

Olifants was the best combiner of the parents for AEGP, with only SST 806 significantly lower. The GCA values for NAEYld were not significantly different. The GCA values for NPE were significantly different, and indicated that Inia and SST 806 had the highest values, followed by Olifants and SST 822, with the other parents significantly lower. The GCA effects for NRE were significantly different, with Olifants and Kariega the parents with the highest GCA values.

Table 5.13 General combining ability (GCA) effects for calculated NUE components of wheat genotypes at two N treatments planted at Bethlehem in 2004

Parents	AEGP[a]	NAEYld[b]	NPE[c]	NRE[d]
Kariega	0.0004	-0.7105	-3.4384	2.9741
Marico	-0.0003	-0.2013	-4.5417	-0.4044
Olifants	0.0020	1.8276	1.68605	6.886
Steenbras	-0.0003	-1.8028	-2.2654	-5.8459
SST 806	-0.0019	0.8439	3.5938	-0.9911
SST 822	0.0008	-0.5231	0.6175	-0.5692
Inia	-0.0007	0.5661	4.1738	-2.0496
LSD (0.05)	0.0054	ns	1.7490	4.0111

[a]AEGP:Agronomic efficiency for grain protein; [b]NAEYld: Agronomic efficiency for grain yield; [c]NPE:Physiological efficiency; [d]NRE: Recovery efficiency.

5.6.4 Specific Combing Ability (SCA) effects for wheat genotypes at Bethlehem

5.6.4.1 Agronomic characteristics

The analysis for the SCA effects for the measured agronomic characteristics are presented in Table 5.14. The SCA values of the hybrids SST 806 x Inia and SST 822 x

Table 5.14 Specific combining ability (SCA) effects for agronomic characteristics of wheat genotypes at two N treatments planted at Bethlehem 2004

F_2-offspring	BM[a]		Yld[b]		HM[c]		TKM[d]		GP[e]		HI[f]	
	LN	HN	LN	HN	LN	HN	LN	HN	LN	HN	LN	HN
Kariega x Marico	80.939	-103.357	0.476	-1.015	-0.952	-1.031	-1.531	-1.206	-0.328	0.417	0.007	-0.041
Kariega x Olifants	-79.371	63.172	-0.364	0.119	-0.333	-1.743	0.688	-1.909	0.161	0.358	-0.002	-0.006
Kariega x Steenbras	175.763	-128.971	1.105	-0.498	1.656	-0.865	2.129	-1.902	-0.574	0.187	0.028	0.004
Kariega x SST 806	-248.295	121.628	-0.886	0.091	-0.819	-1.172	-0.382	-0.843	0.218	0.015	0.033	-0.026
Kariega x SST 822	-55.116	90.442	-0.699	0.218	-0.526	2.435	-1.619	2.624	-0.048	-0.239	-0.040	-0.023
Kariega x Inia	-21.806	2.266	0.061	-0.373	-0.374	-0.080	0.844	-2.131	0.337	0.061	0.015	-0.031
Marico x Olifants	5.065	57.925	0.586	-0.074	0.674	1.598	2.621	2.069	-0.407	-0.378	0.052	-0.021
Marico x Steenbras	103.592	-27.847	0.626	-1.283	-0.537	-0.224	0.329	-0.657	-0.329	-0.366	0.021	-0.084
Marico x SST 806	200.718	219.251	-0.198	1.294	-0.778	1.602	3.018	1.002	-0.024	-0.191	-0.085	0.018
Marico x SST 822	22.250	5.435	1.015	-0.205	2.282	-2.658	-0.619	-3.998	0.240	0.512	0.102	-0.022
Marico x Inia	-180.066	0.216	-1.241	1.004	-0.448	-1.141	-1.893	-0.615	1.047	-0.249	-0.046	0.082
Olifants x Steenbras	89.225	227.008	-0.506	1.071	-0.152	1.031	-2.253	1.706	0.083	-0.055	-0.075	0.007
Olifants x SST 806	-165.639	-39.196	-0.282	0.184	0.141	0.557	0.836	-0.502	0.368	0.110	0.034	0.027
Olifants x SST 822	88.616	-213.439	0.233	-1.226	0.467	-1.869	-0.934	-2.569	-0.034	0.373	-0.011	-0.029
Olifants x Inia	57.430	34.368	0.048	0.356	1.019	2.050	1.095	3.409	-0.166	0.380	-0.012	0.015
Steenbras x SST 806	-148.192	-38.159	-0.100	-0.019	-1.037	0.435	-0.723	1.106	0.427	0.162	0.048	0.015
Steenbras x SST 822	-17.483	156.928	-0.128	1.568	-1.244	1.276	-0.760	2.906	0.524	-0.146	-0.013	0.055
Steenbras x Inia	-102.400	-33.478	-0.059	-0.193	0.174	0.528	2.503	0.883	-0.447	0.225	0.035	-0.002
SST 806 x SST 822	-52.069	-390.820	-0.877	-0.227	1.159	0.626	-0.798	2.174	-0.276	-0.760	-0.100	0.126
SST 806 x Inia	296.571	436.771	1.042	0.519	-0.911	-0.570	-0.548	-1.133	-0.410	0.843	0.020	-0.129
SST 822 x Inia	231.340	765.594	1.711	1.555	-1.485	-0.563	0.681	-1.200	0.468	0.255	0.098	-0.172
LSD (0.05)	280.470	254.556	1.193	11.423	ns	12.753	ns	ns	ns	ns	ns	ns

[a]BM: Biomass; [b]Yld: Grain yield; [c]HM: Hectoliter mass; [d]TKM: Thousand kernel mass; [e]GP: Grain protein percentage; [f]HI: Harvest index.

Inia for BM exceeds the SCA values of the rest of the hybrids at both the LN and HN treatments. It were followed by the hybrids Marico x SST 806 and Olifants x Steenbras (HN). For the measured grain yield, SST 822 x Inia, Kariega x Steenbras, SST 806 x Inia, and Marico x SST 822 were the crosses with the highest SCA values at the LN treatment. Steenbras x SST 822, SST 822 x Inia, and Marico x SST 806 were the best combinations at the HN treatment for grain yield. Jain & Singh (1978) also reported significant SCA effects for yield.

Kariega x SST 822, Olifants x Inia, Marico x SST 806 and Marico x Olifants were the crosses with the highest SCA values for HM at the HN treatment. The SCA values for the LN treatment at HM was non-significant, as well as the values for TKM, GP, and HI, although Paroda *et al*. (1970) showed significant SCA effects for TKM in their results.

5.6.4.2 Calculated Nitrogen uptake components

The results for the SCA effects for the calculated N uptake components are presented in Table 5.15.

Table 5.15 Specific combining ability (SCA) effects for N uptake components of wheat genotypes at two N treatments planted at Bethlehem 2004

F_2-offspring	Ngrain[a]		Ntotal[b]		NHI[c]	
	LN	HN	LN	HN	LN	HN
Kariega x Marico	7.082	-19.552	9.283	-17.501	0.00441	-0.03328
Kariega x Olifants	-5.723	7.365	-4.129	16.519	-0.02378	-0.01657
Kariega x Steenbras	17.499	-10.192	18.093	-13.912	0.02111	0.00269
Kariega x SST 806	-16.230	2.186	-19.822	14.045	0.00826	-0.04413
Kariega x SST 822	-14.459	4.116	-15.525	1.882	-0.01967	-0.00002
Kariega x Inia	3.293	-8.005	1.996	-6.173	0.01530	-0.01924
Marico x Olifants	8.029	-5.451	2.932	-4.726	0.05978	-0.00646
Marico x Steenbras	9.691	-33.001	8.315	-31.866	0.03500	-0.05754
Marico x SST 806	-3.762	27.049	4.743	25.617	-0.07285	0.03365
Marico x SST 822	22.737	0.774	18.495	13.143	0.07189	-0.04291
Marico x Inia	-17.952	21.765	-15.341	15.162	-0.06922	0.06015
Olifants x Steenbras	-9.296	25.817	-5.415	29.992	-0.05619	0.01317
Olifants x SST 806	-3.414	5.724	-7.341	3.364	0.02530	0.01202
Olifants x SST 822	4.637	-26.545	9.130	-29.565	-0.02096	-0.02120
Olifants x Inia	-0.242	12.378	0.093	12.123	0.00133	0.01124
Steenbras x SST 806	1.517	1.648	-1.980	1.623	0.03152	0.00494
Steenbras x SST 822	1.161	36.196	1.468	31.385	-0.00441	0.06072
Steenbras x Inia	-3.814	-3.722	-9.338	-0.734	0.03956	-0.01483
SST 806 x SST 822	-19.469	-16.133	-18.247	-40.000	-0.05941	0.09493
SST 806 x Inia	18.616	23.840	22.130	47.063	0.00985	-0.08433
SST 822 x Inia	37.106	42.429	39.744	74.564	0.06759	-0.11089
LSD (0.05)	24.128	31.171	28.779	35.815	ns	ns

[a]Ngrain: Nitrogen uptake in the grain; [b]Ntotal: Total Nitrogen uptake; [c]NHI: Nitrogen harvest index.

The combinations SST 822 x Inia and SST 806 x Inia had high SCA values at both N treatments for Ngrain and Ntotal. Marico x SST 822 and Kariega x Steenbras also had high SCA values for Ngrain and Ntotal at the LN treatment. Steenbras x SST 822, Marico x SST 806, and Olifants x Steenbras had significantly high values for Ngrain and Ntotal at the HN treatment. The SCA values for NHI were non-significant at both N treatments.

5.6.4.3 Calculated NUE components

The analysis for the SCA effects for the calculated NUE components are presented in Tables 5.16 and 5.17. The SCA values for NupE% at the LN treatment were non-significant. The combinations SST 822 x Inia and SST 806 x Inia had high SCA values at the HN treatment, followed by Steenbras x SST 822 and Olifants x Steenbras. The combinations SST 822 x Inia and SST 806 x Inia had high SCA values at both N treatments for NUEYld indicating specific genes for this component where level of N application did not have a major effect. Marico x SST 822, Kariega x Steenbras, Marico x Steenbras and Marico x Olifants showed high values at the LN treatment for NupE%. Steenbras x SST 822, Marico x SST 806 and Olifants x Steenbras had high SCA values at the HN treatment.

Table 5.16 Specific combining ability (SCA) effects for NUE components of wheat genotypes at two N treatments planted at Bethlehem 2004

F_2-offspring	NupE%[a]		NUEYld[b]		NutEYld[c]	
	LN	HN	LN	HN	LN	HN
Kariega x Marico	7.841	-5.865	4.017	-3.402	1.715	-2.410
Kariega x Olifants	-3.488	5.536	-3.072	0.399	-1.821	-1.486
Kariega x Steenbras	15.282	-4.662	9.330	-1.668	3.111	-0.309
Kariega x SST 806	-16.743	4.707	-7.485	0.306	-0.312	-1.997
Kariega x SST 822	-13.113	0.631	-5.908	0.732	-0.938	0.445
Kariega x Inia	1.686	-2.069	0.513	-1.249	-0.518	-0.986
Marico x Olifants	2.477	-1.584	4.947	-0.248	4.825	0.563
Marico x Steenbras	7.024	-10.679	5.286	-4.300	2.914	-1.697
Marico x SST 806	4.006	8.585	-1.670	4.337	-3.790	1.989
Marico x SST 822	15.622	4.404	8.568	-0.686	2.584	-2.890
Marico x Inia	-12.958	5.081	-10.480	3.365	-7.222	3.088
Olifants x Steenbras	-4.574	10.051	-4.273	3.587	-3.238	0.630
Olifants x SST 806	-6.200	1.127	-2.379	0.617	-0.012	0.172
Olifants x SST 822	7.711	-9.908	1.970	-4.108	-0.900	-1.694
Olifants x Inia	0.078	4.063	0.407	1.193	0.505	-0.424
Steenbras x SST 806	-1.673	0.544	-0.850	-0.063	0.257	-0.247
Steenbras x SST 822	1.240	10.518	-1.080	5.256	-1.905	2.826
Steenbras x Inia	-7.888	-0.246	-0.498	-0.647	3.325	-1.129
SST 806 x SST 822	-15.412	-13.406	-7.402	-0.759	-2.489	6.106
SST 806 x Inia	18.692	15.772	8.800	1.738	2.457	-5.883
SST 822 x Inia	33.571	24.989	14.446	5.210	2.281	-5.591
LSD (0.05)	ns	12.003	10.074	4.769	ns	ns

[a] NupE%: Nitrogen uptake efficiency; [b] NUEYld; Nitrogen use efficiency for grain yield; [c] NutEYld: Nitrogen utilization efficiency for grain yield.

SST 806 x Inia, Kariega x Steenbras, Olifants x Inia, and Steenbras x SST 822 had the highest values for AEGP. Marico x SST 806, Steenbras x SST 822, and Kariega x SST 822 showed high SCA values for NAEYld, followed by Marico x Inia and Olifants x

Steenbras. Marico x SST 806, Steenbras x SST 822, and Kariega x SST 822 had high SCA values for NPE and NRE, with Marico x Inia showing a high value for NPE. Kariega x SST 806 and Olifants x Steenbras had high SCA values for NRE.

Table 5.17 Specific combining ability (SCA) effects for calculated NUE components of wheat genotypes at two N treatments planted at Bethlehem in 2004

F$_2$-offspring	AEGP[a]	NAEYld[b]	NPE[c]	NRE[d]
Kariega x Marico	0.0024	-12.6600	-21.3800	-25.7800
Kariega x Olifants	0.0019	1.0100	0.6800	8.1400
Kariega x Steenbras	0.0049	-6.7600	-10.9500	-11.5000
Kariega x SST 806	-0.0005	3.8200	2.8300	15.6000
Kariega x SST 822	0.0001	8.7400	10.3700	15.7900
Kariega x Inia	-0.0034	0.5500	2.4800	1.8700
Marico x Olifants	-0.0020	-0.9100	2.7700	2.0100
Marico x Steenbras	0.0029	-10.6700	-31.2500	-23.3800
Marico x SST 806	-0.0004	11.2600	13.9400	20.6000
Marico x SST 822	0.0012	-7.7500	-10.7800	-5.4700
Marico x Inia	-0.0025	6.6900	10.0200	8.1800
Olifants x Steenbras	0.0000	6.2900	6.0700	15.1400
Olifants x SST 806	-0.0026	4.3200	4.8500	5.2300
Olifants x SST 822	0.0026	-8.3200	-11.1400	-17.3800
Olifants x Inia	0.0043	-1.7300	-5.2100	-0.9500
Steenbras x SST 806	-0.0006	0.0500	-0.4400	4.2600
Steenbras x SST 822	-0.0040	8.0900	11.5200	14.3200
Steenbras x Inia	0.0040	0.6300	-1.7900	10.5900
SST 806 x SST 822	0.0004	0.2400	0.3000	-0.1500
SST 806 x Inia	0.0051	-0.6300	2.7600	-2.5700
SST 822 x Inia	-0.0039	2.4800	1.4800	5.0300
LSD (0.05)	0.0163	7.8046	5.3434	12.2541

[a]AEGP:Agronomic efficiency for grain protein; [b]NAEYld: Agronomic efficiency for grain yield; [c]NPE:Physiological efficiency; [d]NRE: Recovery efficiency.

5.6.5 General Combing Ability (GCA) effects for wheat genotypes at Vaalharts

5.6.5.1 Agronomic characteristics

The results for the GCA effects for the measured agronomic characteristics are presented in Table 5.18. From the analysis for BM, the HN treatment generally had a significant positive effect on GCA values of the parents, with the exception of Kariega, Steenbras and SST 822, that showed negative responses in GCA values to N applications. Kariega and SST 806 were significantly the best parents at the LN treatment, with SST 806, Olifants and Inia having significantly higher GCA values at the HN treatment. The GCA effects for grain yield were significantly different at both N treatments. The best parents at the LN treatment were Steenbras, Kariega and Olifants, with Marico and Inia at significantly lower GCA values. At the HN treatment, Olifants, Inia and SST 806 were significantly the best parents, with Steenbras significantly lower. Paroda *et al*. (1970) also indicated significant GCA effects for grain yield, indicating that this characteristic is controlled mainly through additive gene action.

Table 5.18 General combining ability (GCA) effects for agronomic characteristics of wheat genotypes at two N treatments planted at Vaalharts in 2004

Parents	BM[a]		Yld[b]		HM[c]		TKM[d]		GP[e]		HI[f]	
	LN	HN	LN	HN	LN	HN	LN	HN	LN	HN	LN	HN
Kariega	46.279	-62.307	0.085	-0.419	1.106	0.566	2.121	1.307	-0.020	0.011	-0.017	-0.021
Marico	-53.472	-5.039	-0.259	-0.107	-0.727	-0.638	-1.005	-1.167	-0.086	-0.109	-0.019	-0.009
Olifants	24.787	80.039	0.051	0.393	-1.216	-0.631	-2.050	-1.141	0.060	-0.051	-0.011	0.017
Steenbras	-9.807	-114.681	0.163	-0.542	0.458	-0.253	0.232	-0.904	-0.030	-0.102	0.058	-0.023
SST 806	34.413	122.567	0.028	0.290	0.288	-0.057	0.343	-0.422	-0.039	-0.111	-0.021	-0.005
SST 822	1.761	-49.053	0.041	0.039	0.084	0.351	0.313	1.067	0.077	0.154	0.005	0.018
Inia	-43.962	28.474	-0.109	0.347	0.006	0.662	0.047	1.259	0.037	0.208	0.005	0.023
LSD (0.05)	55.369	104.034	0.186	0.278	1.002	0.830	1.709	1.214	ns	ns	0.035	0.025

[a]BM: Biomass; [b]Yld: Grain yield; [c]HM: Hectoliter mass; [d]TKM: Thousand kernel mass; [e]GP: Grain protein percentage; [f]HI: Harvest index.

The GCA effects for hectolitre mass were significant for both N treatments. With the exception of Inia and SST 822, the other parents showed reduced GCA values for HM at the HN treatment. Kariega, Steenbras and SST 806 had significantly higher GCA values at the LN treatment, with the significantly lowest values for Olifants and Marico. At the HN treatment Inia, Kariega and SST 822 had significantly higher values with Marico, Olifants and Steenbras at lower values.

Similarly to Jain & Singh (1970) and Singh *et al*. (1986) that calculated significant GCA effects for TKM, in this study Kariega was the best parent, with only Olifants significantly lower than the other parents at the LN treatment. Kariega, SST 822 and Inia had significantly higher GCA values at the HN treatment. In contrast to Mihaljev & Kovacev-Djolai (1978) that showed significant GCA effects for grain protein content, the GCA values for GP at both N treatments were non-significant. The GCA values for HI were significant for both N treatments, and at the LN treatment, Steenbras had the highest value, followed by SST 822 and Inia, with the other parents significantly lower. At the HN treatment, Inia, SST 822 and Olifants did not differ significantly and had the highest GCA values for HI.

5.6.5.2 Calculated Nitrogen uptake components

The analysis for the GCA effects for the calculated N uptake components are presented in Table 5.19.

Table 5.19 General combining ability (GCA) effects for N uptake components of wheat genotypes at two N treatments planted at Vaalharts in 2004

Parents	Ngrain[a]		Ntotal[b]		NHI[c]	
	LN	HN	LN	HN	LN	HN
Kariega	1.424	-8.891	1.951	-8.700	-0.003	-0.026
Marico	-4.926	-2.972	-5.760	-1.545	-0.013	-0.018
Olifants	1.139	7.914	1.378	5.130	0.004	0.039
Steenbras	2.826	-11.923	2.728	-10.568	0.016	-0.053
SST 806	0.489	5.294	0.464	7.029	0.002	0.010
SST 822	0.965	1.745	1.602	0.459	-0.003	0.017
Inia	-1.917	8.833	-2.363	8.196	-0.003	0.031
LSD (0.05)	3.348	6.270	4.232	8.944	ns	0.028

[a]Ngrain: Nitrogen uptake in the grain; [b]Ntotal: Total Nitrogen uptake; [c]NHI: Nitrogen harvest index.

Nitrogen application had a significant effect on the N uptake components. Steenbras had the highest GCA value for Ngrain and Ntotal at the LN treatment, but the lowest at the HN treatment. Kariega and Olifants had high values at the LN treatment, with Inia, Olifants and SST 806 with the highest GCA values for Ngrain at the HN treatment.

Kariega, SST 822 and Olifants had the best values at the LN treatment for Ntotal, with Inia, SST 806 and Olifants the best parents at the HN treatment for both Ntotal and NHI.

5.6.5.3 Calculated NUE components

The analysis for the GCA effects for the calculated NUE components are presented in Tables 5.20 and 5.21. All the components indicated significant variability except for AEGP. The parents Steenbras, SST 822, Kariega and Olifants had significantly the highest values for NupE% at the LN treatment, with Inia, SST 806 and Olifants the best parents at the HN treatment. Steenbras was the best parent for NUEYld at the LN treatment, followed by Kariega. Olifants, Inia, and SST 806 were the best parents at the HN treatment. Olifants and Inia were the best parents for NutEYld at the HN treatment.

Table 5.20 General combining ability (GCA) effects for NUE components of wheat genotypes at two N treatments planted at Vaalharts in 2004

Parents	NupE%[a]		NUEYld[b]		NutEYld[c]	
	LN	HN	LN	HN	LN	HN
Kariega	2.487	-3.366	1.088	-1.623	-0.137	-1.211
Marico	-7.341	-0.598	-3.305	-0.414	-0.367	-0.548
Olifants	1.757	1.985	0.650	1.521	-0.008	1.934
Steenbras	3.477	-4.089	2.083	-2.098	0.959	-2.277
SST 806	0.591	2.719	0.355	1.123	0.325	0.777
SST 822	2.042	0.178	0.519	0.150	-0.420	0.386
Inia	-3.012	3.171	-1.390	1.342	-0.351	0.938
LSD (0.05)	5.394	3.461	2.374	1.076	ns	1.622

[a]NupE%: Nitrogen uptake efficiency; [b]NUEYld; Nitrogen use efficiency for grain yield; [c]NutEYld: Nitrogen utilization efficiency for grain yield.

Table 5.21 General combining ability (GCA) effects for calculated NUE components of wheat genotypes at two N treatments planted at Vaalharts in 2004

Parents	AEGP[a]	NAEYld[b]	NPE[c]	NRE[d]
Kariega	0.0001	-2.877	-3.208	-6.121
Marico	-0.0002	0.772	0.603	2.138
Olifants	-0.0005	2.160	3.362	2.622
Steenbras	-0.0002	-3.368	-7.468	-6.138
SST 806	-0.0005	1.014	2.160	2.703
SST 822	0.0004	0.210	1.509	-0.127
Inia	0.0009	2.088	3.042	4.922
LSD (0.05)	ns	1.663	2.715	4.929

[a]AEGP:Agronomic efficiency for grain protein; [b]NAEYld: Agronomic efficiency for grain yield; [c]NPE:Physiological efficiency; [d]NRE: Recovery efficiency.

Table 5.22 Specific combining ability (SCA) effects for agronomic characteristics of wheat genotypes at two N treatments planted at Vaalharts in 2004

F_2-offspring	BM[a]		Yld[b]		HM[c]		TKM[d]		GP[e]		HI[f]	
	LN	**HN**	**LN**	**HN**	**LN**	**HN**	**LN**	**HN**	**LN**	**HN**	**LN**	**HN**
Kariega x Marico	6.652	-241.375	0.117	-0.963	-0.906	-0.120	-1.113	-0.791	0.027	0.501	0.017	-0.031
Kariega x Olifants	141.060	2.175	0.418	0.115	1.317	1.439	2.398	2.017	-0.179	-0.477	-0.010	0.008
Kariega x Steenbras	-79.420	-52.789	-0.630	-0.188	-1.024	-1.006	-1.083	-1.887	0.135	0.227	-0.085	-0.002
Kariega x SST 806	105.297	-67.264	0.108	0.047	0.646	0.065	1.406	-0.169	0.250	-0.320	-0.025	0.020
Kariega x SST 822	6.366	157.626	0.214	0.293	1.217	-0.143	2.102	0.809	-0.022	0.127	0.030	-0.012
Kariega x Inia	46.449	236.719	0.263	0.767	0.494	1.280	-0.565	1.617	-0.055	0.101	0.023	0.005
Marico x Olifants	-15.129	7.373	0.037	-0.561	0.683	-0.991	1.057	0.024	-0.130	0.367	0.024	-0.049
Marico x Steenbras	108.111	68.843	0.290	0.621	0.809	0.631	1.309	-0.080	-0.330	0.161	-0.042	0.041
Marico x SST 806	-120.485	-44.528	-0.477	0.036	-0.287	-0.231	0.198	0.439	-0.198	0.347	-0.006	0.014
Marico x SST 822	32.727	211.121	0.028	0.870	0.650	1.261	1.028	1.550	-0.417	-0.346	-0.020	0.014
Marico x Inia	-54.942	242.466	-0.212	1.183	-0.433	-0.330	-1.393	-0.319	0.256	-0.253	0.012	0.051
Olifants x Steenbras	118.336	183.912	0.317	0.208	-0.102	-0.609	-0.646	-0.906	0.221	-0.197	-0.043	-0.020
Olifants x SST 806	-25.021	-203.299	-0.029	-0.604	-1.198	-0.572	-1.824	-0.987	0.536	-0.112	0.014	-0.010
Olifants x SST 822	-198.362	-201.813	-0.663	-0.477	-0.094	0.487	-0.128	0.191	-0.009	0.390	0.017	0.017
Olifants x Inia	77.374	376.854	0.351	0.746	0.517	-0.157	1.072	-0.602	-0.246	-0.274	0.013	-0.037
Steenbras x SST 806	54.463	35.354	-0.036	1.017	1.628	1.350	3.961	1.576	-0.157	0.036	-0.068	0.072
Steenbras x SST 822	42.515	-84.760	0.458	-0.084	-0.902	-0.257	-0.943	-0.713	-0.189	0.234	0.053	0.015
Steenbras x Inia	41.842	68.150	0.101	0.123	0.409	1.065	1.257	2.828	0.101	0.104	-0.032	-0.003
SST 806 x SST 822	-177.110	229.423	-0.152	-0.331	-2.437	-1.304	-7.722	-1.074	0.463	-0.938	0.144	-0.080
SST 806 x Inia	177.217	-360.572	0.255	-0.392	2.185	2.119	7.881	2.159	-0.964	0.790	-0.127	0.042
SST 822 x Inia	69.776	-364.322	-0.336	-0.011	1.289	1.678	5.978	1.537	-0.340	1.811	-0.168	0.094
LSD (0.05)	169.156	317.828	0.569	0.850	ns	ns	ns	ns	ns	ns	ns	ns

[a] BM: Biomass; [b] Yld: Grain yield; [c] HM: Hectoliter mass; [d] TKM: Thousand kernel mass; [e] GP: Grain protein percentage; [f] HI: Harvest index.

5.6.6 Specific Combing Ability (SCA) effects for wheat genotypes at Vaalharts

5.6.6.1 Agronomic characteristics

The results for the SCA effects for the measured agronomic characteristics are presented in Table 5.22. The N applications resulted in significant differences in SCA values for biomass (BM) and grain yield. The best hybrid for BM at LN was SST 806 x Inia, followed by Kariega x Olifants, Olifants x Steenbras and Marico x Steenbras. At the HN treatment, Olifants x Inia had the highest SCA value, followed by Marico x Inia, Kariega x Inia, SST 806 x SST 822, and Marico x SST 822.

The best hybrid combination for grain yield at the LN treatment was Steenbras x SST 822, followed by Kariega x Olifants, Olifants x Inia, and Marico x Steenbras. At the HN treatment, Marico x Inia was the combination with the highest SCA value, with Steenbras x SST 806, Marico x SST 822 and Kariega x Inia not significantly different. Jain & Singh (1978) reported significant SCA effects for yield, indicating that non-additive gene action can result in specific hybrid combinations better adapted to environmental conditions. The SCA values for HM, TKM, GP and HI were not significant at both N treatments, although Paroda *et al*. (1970) reported significant SCA values for TKM in their studies.

5.6.6.2 Calculated Nitrogen uptake components

The analysis results for the SCA effects for the calculated N uptake components are presented in Table 5.23.

Table 5.23 Specific combining ability (SCA) effects for N uptake components of wheat genotypes at two N treatments planted at Vaalharts in 2004

F_2-offspring	Ngrain[a]		Ntotal[b]		NHI[c]	
	LN	HN	LN	HN	LN	HN
Kariega x Marico	2.189	-17.758	2.138	-19.508	0.014	-0.061
Kariega x Olifants	6.739	-0.707	8.397	-3.871	0.004	0.024
Kariega x Steenbras	-10.853	-3.204	-10.629	-3.240	-0.062	-0.004
Kariega x SST 806	2.769	-0.961	4.731	-9.128	-0.017	0.043
Kariega x SST 822	3.981	7.067	1.849	13.630	0.050	-0.015
Kariega x Inia	4.716	17.112	5.858	28.848	0.008	-0.005
Marico x Olifants	0.253	-10.215	0.589	-2.038	-0.006	-0.070
Marico x Steenbras	3.924	14.082	5.714	13.727	-0.010	0.060
Marico x SST 806	-8.908	3.254	-10.851	4.651	-0.008	0.002
Marico x SST 822	-0.573	16.007	-1.891	14.834	0.014	0.043
Marico x Inia	-3.138	24.243	-3.849	23.767	-0.002	0.090
Olifants x Steenbras	6.740	3.070	9.933	9.727	-0.019	-0.008
Olifants x SST 806	1.324	-13.263	1.042	-20.891	0.013	0.003
Olifants x SST 822	-12.063	-7.161	-17.031	-15.114	0.029	0.029
Olifants x Inia	5.409	13.565	6.706	22.359	0.003	-0.021
Steenbras x SST 806	-1.372	21.354	-0.742	16.050	-0.020	0.092
Steenbras x SST 822	7.518	-0.554	7.349	-3.881	0.029	0.027
Steenbras x Inia	2.071	2.866	3.995	8.291	-0.022	-0.007
SST 806 x SST 822	-1.667	-11.011	-0.600	5.053	-0.011	-0.166
SST 806 x Inia	1.965	-4.870	0.865	-20.698	0.010	0.119
SST 822 x Inia	-7.261	9.333	-10.308	-3.707	-0.015	0.139
LSD (0.05)	10.228	18.155	12.929	27.325	ns	0.085

[a] Ngrain: Nitrogen uptake in the grain; [b] Ntotal: Total Nitrogen uptake; [c] NHI: Nitrogen harvest index.

The SCA effects for Ngrain and Ntotal at both N treatments were significant, and showed that the crosses Kariega x Inia and Olifants x Inia had high values. The crosses Steenbras x SST 822, Kariega x Olifants, Olifants x Steenbras had high SCA values for Ngrain and Ntotal at the LN treatment. In contrast, Marico x Inia had a high value at the HN treatment, followed by Steenbras x SST 806, Marico x SST 822 and Marico x Steenbras. SST 822 x Inia and SST 806 x Inia showed the highest SCA values for NHI at the HN treatment, followed by Steenbras x SST 806 and Marico x Inia.

5.6.6.3 Calculated NUE components

The analysis results for the SCA effects for the calculated NUE components are presented in Tables 5.24 and 5.25. Significant SCA values were calculated for NupE% and NUEYld. The crosses Kariega x Inia, Marico x Steenbras and Olifants x Inia showed high SCA values at both N treatments for NupE% and NUEYld. The crosses Kariega x Olifants, Olifants x Steenbras, and Steenbras x SST 822 had high values at the LN treatment for both components. Crosses that showed high SCA values at HN were Marico x Inia, Steenbras x SST 806 and Marico x SST 822. No significant differences were found for NutEYld.

Table 5.24 Specific combining ability (SCA) effects for NUE components of wheat genotypes at two N treatments planted at Vaalharts in 2004

F$_2$-offspring	NupE%[a]		NUEYld[b]		NutEYld[c]	
	LN	HN	LN	HN	LN	HN
Kariega x Marico	2.724	-7.548	1.485	-3.724	0.664	-4.101
Kariega x Olifants	10.703	-1.498	5.330	0.443	0.914	2.420
Kariega x Steenbras	-13.547	-1.254	-8.021	-0.727	-3.975	-0.437
Kariega x SST 806	6.030	-3.532	1.375	0.181	-2.024	2.848
Kariega x SST 822	2.357	5.274	2.721	1.132	2.797	-1.119
Kariega x Inia	7.467	11.161	3.349	2.965	0.646	-0.417
Marico x Olifants	0.751	-0.789	0.467	-2.172	0.070	-4.063
Marico x Steenbras	7.283	5.311	3.702	2.402	0.901	2.429
Marico x SST 806	-13.830	1.800	-6.083	0.140	0.736	-0.903
Marico x SST 822	-2.411	5.739	0.361	3.365	2.436	2.886
Marico x Inia	-4.906	9.196	-2.704	4.577	-1.205	4.707
Olifants x Steenbras	12.661	3.763	4.039	0.806	-2.001	0.167
Olifants x SST 806	1.328	-8.083	-0.362	-2.337	-1.470	0.458
Olifants x SST 822	-21.706	-5.848	-8.454	-1.845	1.470	0.181
Olifants x Inia	8.546	8.650	4.480	2.885	1.180	-0.295
Steenbras x SST 806	-0.946	6.210	-0.459	3.936	-0.489	4.253
Steenbras x SST 822	9.366	-1.502	5.841	-0.325	2.344	0.680
Steenbras x Inia	5.091	3.208	1.286	0.477	-1.573	-0.578
SST 806 x SST 822	-0.764	1.955	-1.941	-1.276	-2.373	-5.697
SST 806 x Inia	1.103	-8.009	3.252	-1.520	4.250	3.870
SST 822 x Inia	-13.138	-1.435	-4.293	-0.047	0.264	2.124
LSD (0.05)	16.479	10.572	7.254	3.288	ns	ns

[a]NupE%: Nitrogen uptake efficiency; [b]NUEYld; Nitrogen use efficiency for grain yield; [c]NutEYld: Nitrogen utilization efficiency for grain yield.

Table 5.25 Specific combining ability (SCA) effects for calculated NUE components of wheat genotypes at two N treatments planted at Vaalharts in 2004

F_2-offspring	AEGP[a]	NAEYld[b]	NPE[c]	NRE[d]
Kariega x Marico	0.0027	-5.934	-11.29	-11.85
Kariega x Olifants	-0.0018	-1.959	0.28	-7.38
Kariega x Steenbras	0.0004	1.892	6.54	2.83
Kariega x SST 806	-0.0031	0.097	4.69	-6.78
Kariega x SST 822	0.0009	0.208	-2.87	6.01
Kariega x Inia	0.0009	3.233	0.87	13.69
Marico x Olifants	0.0026	-3.591	-6.30	-2.02
Marico x Steenbras	0.0026	1.273	5.58	3.18
Marico x SST 806	0.0031	3.288	1.19	9.53
Marico x SST 822	0.0004	4.446	3.25	8.76
Marico x Inia	-0.0001	2.191	1.73	4.24
Olifants x Steenbras	-0.0012	1.502	0.19	4.54
Olifants x SST 806	-0.0037	-3.097	-0.01	-12.01
Olifants x SST 822	0.0020	0.475	1.48	-0.21
Olifants x Inia	-0.0002	2.289	-0.83	8.87
Steenbras x SST 806	0.0009	5.658	10.36	8.80
Steenbras x SST 822	0.0026	-1.228	0.19	-1.83
Steenbras x Inia	-0.0002	-0.070	1.90	1.85
SST 806 x SST 822	0.0025	0.804	-4.65	9.64
SST 806 x Inia	-0.0005	-7.775	-3.89	-23.28
SST 822 x Inia	0.0016	0.297	0.64	-2.42
LSD (0.05)	ns	5.080	8.29	15.06

[a] AEGP:Agronomic efficiency for grain protein; [b] NAEYld: Agronomic efficiency for grain yield; [c] NPE:Physiological efficiency; [d] NRE: Recovery efficiency.

Significant differences were calculated for NAEYld, NPE and NRE. The crosses that showed the highest SCA values for NAEYld were Steenbras x SST806, Marico x SST 822, Marico x SST 806 and Kariega x Inia. Steenbras x SST 806 had the highest value for NPE, followed by Kariega x Steenbras and Marico x Steenbras. For the NRE component, the best combinations were Kariega x Inia, SST 806 x SST 822, Marico x SST 806, Olifants x Inia and Steenbras x SST 806.

5.6.7 Calculated GCA:SCA ratios for measured and calculated components

These ratios reveal whether the characteristics and components show an additive or non-additive gene action. A GCA:SCA ratio with a value greater than one, indicates additive gene action, whereas a GCA:SCA ratio with a value lower than one indicates dominant gene action. A high SCA to GCA ratio is an indication of over dominance. Additive gene action also indicates that a characteristic can be improved through selection procedures, and less environmental interactions are found for this gene action. In Table 5.26 the calculated GCA:SCA ratios for the respective components at Bethlehem are listed.

At the LN treatment, BM, TKM, GP and NutEYld showed additive gene action with ratios above one. The GCA:SCA ratios of most of the components increased at the HN treatment, with only grain yield, Ngrain and NUEYld at values less than one. In particular, TKM had a high ratio a the LN treatment, which decreased at the HN treatment. This can be attributed to the high heritability of this component, and the expression of seed size is not to a great extent affected by environment. Grain protein showed an increased ratio at the HN treatment which indicate that selection at both N treatments, but specifically at an increased N level, can be beneficial as N has an effect on additive gene expression for this component. Hectolitre mass also showed an increased ratio at the HN treatment, as did the ratio for BM. Sayed (1978) reported that grain yield was the only character in their studies with more non-additive than additive gene action.

Table 5.26 Calculated GCA:SCA ratios for measured and calculated components at two N treatments in a wheat trial planted at Bethlehem in 2004

Component	Nitrogen treatments					
	LN			HN		
	GCA	SCA	GCA:SCA	GCA	SCA	GCA:SCA
Agronomic components						
BM	60189.8	57452.8	1.048	88609.0	61145.7	1.449
Yld	0.345	1.568	0.220	1.483	2.083	0.712
HM	2.543	3.086	0.824	12.039	6.923	1.739
TKM	69.985	8.798	7.955	35.296	14.638	2.411
GP	0.837	0.458	1.825	1.754	0.308	5.699
HI	0.006	0.006	0.987	0.006	0.004	1.561
Nitrogen uptake components						
Ngrain	103.760	592.128	0.175	882.175	1086.438	0.812
Ntotal	269.059	683.291	0.394	1480.061	1263.030	1.172
NHI	0.004	0.004	0.899	0.009	0.003	3.323
NUE components						
NupE%	191.964	487.493	0.394	166.230	141.856	1.172
NUEYld	24.637	111.860	0.220	16.657	23.396	0.712
NutEYld	28.906	20.023	1.444	19.793	8.556	2.313
AEGP	0.0001	0.0001	1.000			
NAEYld	12.663	48.350	0.262			
NPE	107.642	152.604	0.705			
NRE	144.160	199.304	0.723			

The N uptake components Ntotal and NHI only showed increased ratios at the HN treatment, indicating that selection for these components must be done at high N availability. The NUE component NutEYld had a ratio of above one at both N treatments, with an increased ratio at the higher N application indicating that additive gene effects more pronounced at the higher N availability. The component NupE% also showed a higher ratio at the HN treatment. The calculated NUE components NAEYld, NPE and NRE showed non-additive gene action.

In Table 5.27 the calculated GCA:SCA ratios for the respective components at Vaalharts are listed. The components BM, grain yield, HM, TKM and HI showed additive gene action with ratios above one at the LN treatment. At the HN treatment, the ratios for BM, grain yield, HM, TKM, GP and HI were further increased, indicating that at this environment selection under applied N fertilizer will be beneficial for additive gene expression.

Table 5.27 Calculated GCA:SCA ratios for measured and calculated components at two N treatments in a wheat trial planted at Vaalharts in 2004

Component	Nitrogen treatments					
	LN			HN		
	GCA	SCA	GCA:SCA	GCA	SCA	GCA:SCA
Agronomic components						
BM	39742.4	29785.4	1.334	187672.6	99703.7	1.882
Yld	0.532	0.368	1.443	3.789	1.081	3.505
HM	15.888	2.553	6.223	7.889	2.332	3.383
TKM	44.913	9.261	4.850	36.406	5.222	6.971
GP	0.095	0.192	0.493	0.470	0.421	1.118
HI	0.021	0.006	3.639	0.010	0.003	2.990
Nitrogen uptake components						
Ngrain	181.896	116.228	1.565	1807.934	461.931	3.914
Ntotal	246.091	193.432	1.272	1497.898	801.129	1.870
NHI	0.002	0.002	0.884	0.030	0.006	4.992
NUE components						
NupE%	399.761	314.220	1.272	224.228	119.925	1.870
NUEYld	86.355	59.847	1.443	56.710	16.179	3.505
NutEYld	6.648	11.853	0.561	55.462	16.128	3.439
AEGP	0.0001	0.0001	1.000			
NAEYld	45.470	11.855	3.836			
NPE	140.877	29.674	4.747			
NRE	177.194	92.418	1.917			

The N uptake components Ngrain and Ntotal had ratios above one at the LN and HN treatments, and NHI showed an increased value at the HN treatment. The calculated NUE components NupE% and NUEYld showed ratios above one at the LN treatment, and together with NutEYld had increased ratios at the HN treatment. In contrast to the response calculated at Bethlehem, the calculated components NAEYld, NPE and NRE showed additive gene action.

These differences in response between the two environments can be attributed to the different growing conditions and N availability scenarios as measured at planting, inducing the changes in agronomic and NUE components. In the semi-dwarf cultivars originating from CIMMYT the increase in yields have been associated with gains in both NUE components: uptake and utilization efficiency at the medium to high levels of N fertility, and only with uptake efficiency under low N fertility. This suggests that the level of N in the soil plays a very important role in the genetic expression of uptake and utilization efficiency in wheat (Ortiz-Monasterio *et al.*, 1997).

5.6.8 Calculated heritability values

The broad- and narrow-sense heritability values were calculated for all the measured and calculated components, and the results are presented in Tables 5.28 and 5.29 for Bethlehem and Vaalharts respectively.

5.6.8.1 Bethlehem

At the LN treatment, all the measured agronomic characteristics showed meaningful broad-sense heritability values, and only TKM and GP had mentionable narrow-sense heritability values. At the HN treatment, all the agronomic characteristics showed increased broad-sense heritability values compared to the LN treatment, except for TKM that had reduced broad- and narrow-sense heritability values. The component GP had a higher narrow-sense heritability value at the HN treatment compared to the LN treatment. These responses in heritability values at different N levels, indicate that the gene expression for these components were higher when available N was sufficient.

The N uptake and NUE components all showed acceptable broad-sense heritabilities at the LN treatment, but no significant response in narrow-sense values. The broad-sense heritability values were higher at the HN treatment for Ngrain, Ntotal, NHI, NupE%, NUEYld and NutEYld. The components NHI and NutEYld also had high narrow-sense heritabilities. The calculated NUE components AEGP, NAEYld, NPE and NRE also had

Table 5.28 Additive and dominance variance components and calculated broad and narrow sense heritability of agronomic and N use efficiency components of wheat genotypes at two N treatments at Bethlehem

	Nitrogen treatments											
		LN						HN				
Components	Additive variance	Dominance variance	Environmental variance	Phenotypic variance	Broad sense Heritability	Narrow sense Heritability	Additive variance	Dominance variance	Environmental variance	Phenotypic variance	Broad sense Heritability	Narrow sense Heritability
Agronomic characteristics												
BM	396.6084	8445.5979	9832.9419	18675.1482	0.4735	0.0212	2233.9442	11383.7656	8099.8185	21717.5283	0.6270	0.1029
Yld	-0.0927	0.3545	0.1778	0.4396	0.5955	-	-0.0388	0.4156	0.2532	0.6300	0.5981	-
HM	-0.0343	0.3880	0.6140	0.9676	0.3655	-	0.4004	1.2637	0.9476	2.6117	0.6372	0.1533
TKM	4.5304	0.4850	2.4567	7.4721	0.6712	0.6063	1.5724	1.8725	2.8168	6.2617	0.5502	0.2511
GP	0.0294	0.0529	0.0938	0.1761	0.4673	0.1668	0.1081	0.0157	0.0827	0.2064	0.5994	0.5235
HI	-0.0001	0.0011	0.0012	0.0023	0.4522	-	0.0002	0.0006	0.0008	0.0015	0.4779	0.1061
Nitrogen uptake components												
Ngrain	-37.3562	129.9169	72.7725	165.3333	0.5598	-	-12.5936	229.2760	121.4533	338.1358	0.6408	-
Ntotal	-30.6865	124.2492	103.5264	197.0890	0.4747	-	20.2826	241.7392	160.3426	422.3645	0.6204	0.0480
NHI	-0.0001	0.0007	0.0009	0.0016	0.4000	-	0.0005	0.0004	0.0006	0.0015	0.5697	0.3263
Nitrogen use efficiency components												
NupE%	-21.8930	88.6447	73.8617	140.6135	0.4747	-	2.2779	27.1507	18.0086	47.4372	0.6204	0.0480
NUEYld	-6.6146	25.2923	12.6857	31.3634	0.5955	-	-0.4352	4.6676	2.8433	7.0757	0.5982	-
NutEYld	0.6648	1.9819	4.6618	7.3085	0.3621	0.0910	0.8401	0.8162	2.0009	3.6573	0.4529	0.2297
Calculated NUE components												
AEGP	0.000001	0.000006	0.000003	0.00001	0.7000	0.1000						
NAEYld	-7.93047	40.73594	7.61392	40.4194	0.8116	-						
NPE	-9.99157	141.89655	10.70737	142.6124	0.9249	-						
NRE	-12.25416	142.99170	56.31231	187.0498	0.6989	-						

- : negative values

Table 5.29 Additive and dominance variance components and calculated broad and narrow sense heritability of agronomic and N use efficiency components of wheat genotypes at two N treatments at Vaalharts

	Nitrogen treatments											
	LN						HN					
Components	Additive variance	Dominance variance	Environmental variance	Phenotypic variance	Broad sense Heritability	Narrow sense Heritability	Additive variance	Dominance variance	Environmental variance	Phenotypic variance	Broad sense Heritability	Narrow sense Heritability
Agronomic characteristics												
BM	829.1841	5939.4450	3576.7031	10345.3322	0.6543	0.0802	6335.7363	21419.8972	12626.8072	40382.4407	0.6873	0.1569
Yld	0.0126	0.0801	0.0405	0.1332	0.6959	0.0944	0.2008	0.2690	0.0903	0.5601	0.8388	0.3585
HM	0.9965	-0.3606	1.1723	1.8083	0.3517	0.5511	0.4198	-0.0632	0.8068	1.1634	0.3065	0.3608
TKM	2.6611	-0.4105	3.4065	5.6571	0.3978	0.4704	2.3260	-0.0507	1.7191	3.9944	0.5696	0.5823
GP	-0.0086	0.0076	0.0629	0.0618	-0.0176	-	0.0026	0.0443	0.1008	0.1477	0.3176	0.0174
HI	0.0011	0.0005	0.0041	0.0057	0.2783	0.1980	0.0005	0.0003	0.0007	0.0016	0.5390	0.3218
Nitrogen uptake components												
Ngrain	5.1144	24.5419	13.0754	42.7317	0.6940	0.1197	98.8924	111.7636	45.8651	256.5211	0.8212	0.3855
Ntotal	4.4266	41.2164	20.8945	66.5374	0.6860	0.0665	46.9162	194.8462	93.3304	335.0927	0.7215	0.1400
NHI	0.0000	0.0001	0.0007	0.0008	0.1199	-	0.0018	0.0010	0.0009	0.0037	0.7593	0.4820
Nitrogen use efficiency components												
NupE%	7.1906	66.9533	33.9429	108.0867	0.6860	0.0665	7.0231	29.1678	13.9711	50.1620	0.7215	0.1400
NUEYld	2.0428	13.0148	6.5775	21.6351	0.6960	0.0944	3.0057	4.0262	1.3514	8.3834	0.8388	0.3585
NutEYld	-0.4392	0.5573	3.6349	3.7530	0.0315	-	2.9165	2.2934	3.0699	8.2798	0.6292	0.3522
Calculated NUE components												
AEGP	-0.000001	0.000001	0.000006	0.00001	0.0000	-						
NAEYld	7.47019	8.62805	3.22630	19.3245	0.8330	0.3866						
NPE	24.70264	21.07263	8.59685	54.3721	0.8419	0.4543						
NRE	18.84184	64.07002	28.34270	111.2546	0.7452	0.1694						

- : negative values

high broad-sense heritability values. These results indicate significant responses in heritabilities for most of the components.

5.6.8.2 Vaalharts

The measured agronomic components grain yield and BM showed the highest broad-sense heritability values at the LN treatment, followed by TKM, HM and HI. Only HM and TKM had significantly high narrow-sense values at the LN treatment. At the HN treatment high broad-sense values were found for grain yield, BM, TKM and HI, with mentionable narrow-sense heritability values. Except for HM, higher broad- and narrow-sense heritability values were calculated in response to the N application at the HN treatment.

The N uptake components Ngrain and Ntotal had high broad-sense heritability values at the LN treatment, The broad-sense heritability values for Ngrain, Ntotal and NHI increased in response to the HN treatment, and the narrow-sense heritability values for Ngrain and Ntotal were also increased.

The NUE components NupE and NUEYld had high broad-sense values at the LN treatments. The broad-sense heritability values were increased at the HN treatment at NupE, NUEYld and NHI, as were the narrow-sense values. The calculated NUE components NAEYld, NPE and NRE showed high broad-sense heritability values, with the narrow-sense values for NAEYld and NPE also notably high.

5.7 Conclusions

Results collected at the two tested localities indicated significant GCA effects for the parental cultivars at the majority of measured agronomic and NUE components at both N treatments. Significant SCA effects for the tested hybrids were also found at BM, grain yield, Ngrain, Ntotal, NupE%, NUEYld, NAEYld, PHE and NRE. The application of N fertilizer (LN versus HN treatments) significantly affected the significance of the calculated combining abilities.

For the agronomic characteristics that were measured at Bethlehem, GCA effects for BM, HM, TKM, GP and HI were significant at the HN treatment. Significant GCA effects were found at the LN treatment for TKM and GP. The N uptake components showed significant GCA effects for Ngrain, Ntotal and NHI at the HN treatment. For the NUE efficiency components significant GCA effects were calculated for NupE%, NUEYld and NutEYld at the HN treatment. No significant cultivar differences were found for the N uptake and NUE components at the LN treatment. For the agronomic components SST 822, Inia and Kariega generally had the highest GCA values. The cultivars Marico, Olifants, SST 806 and Inia showed the highest GCA values at the HN treatment for the agronomic, N uptake and NUE components.

At Vaalharts significant GCA effects for the agronomic components BM, grain yield, HM, TKM and HI were found at both N treatments. For the N uptake components, significant GCA effects were calculated for Ngrain and Ntotal at both N treatments and for NHI at the HN treatment. Significant GCA effects were found for the NUE components NupE%, NUEYld at both N treatments and for NutEYld at the HN treatment. The cultivars Kariega, Olifants, Inia, Steenbras and SST 806 had the highest GCA values for the agronomic, N uptake and NUE components at the LN treatment. At the HN treatment Olifants, SST 806 and Inia had the highest GCA values for these components, as well as for the N uptake and NUE components.

The parental cultivars showed genetic variability for the measured components. This indicate that selection of parents for the different NUE components are possible because sufficient genetic variability exists, but selections will differ according to the specific component and target environment. The selection of parental cultivars for these components will also be more effective under high N availability.

The calculated SCA effects at Bethlehem were significant for BM, grain yield, Ngrain, Ntotal, NUEYld at both N treatments, for NUE components NAEYld, NPE and NRE, and for HM and NupE% at the HN treatment. The crosses that showed the highest SCA values for the agronomic components at both N treatments were Marico x SST 806, SST 806 x Inia, and SST 822 x Inia. At the HN treatment the crosses Olifants x Steenbras, Steenbras x SST 822 and Marico x Inia had the highest SCA values. The N uptake components showed the crosses Kariega x Steenbras and Marico x SST 822 at high SCA values at the LN treatment. At the HN treatment Marico x SST 806, Marico x Inia, Olifants x SST 806 and SST 806 x SST 822 at high SCA values for these components. The crosses SST 806 x Inia and SST 822 x Inia had high SCA values at both N treatments. For the NUE components Kariega x Steenbras, Marico x Olifants and Marico x Steenbras showed high SCA values at the LN treatment. For these components at the HN treatment, the crosses Marico x SST 806, Marico x Inia, Olifants x Steenbras, Steenbras x SST 822, SST 806 x Inia and SST 822 x Inia had the highest SCA values.

At Vaalharts significant SCA effects were calculated for BM, grain yield, Ngrain, Ntotal, NupE%, NUEYld at both N treatments and for NHI at the HN treatment. The crosses Kariega x Olifants, SST 806 x Inia and Kariega x SST 806 had high SCA value at the LN treatment for the agronomic components. Marico x Inia, Kariega x SST 822 and Marico x SST 822 showed high SCA values for these components at the HN treatment. Olifants x Inia, Kariega x Inia and Olifants x Steenbras had high SCA values at both N treatments. For the N uptake and NUE components Kariega x Olifants and Steenbras x SST 822 had high SCA values at the LN treatment, with Kariega x SST 822, Marico x SST 822, Marico x Inia and Steenbras x SST 806 high values at the HN treatment. The crosses Kariega x Inia, Marico x Steenbras, Olifants x Steenbras and Olifants x Inia had high SCA values at both N treatments for these components.

The calculated GCA:SCA ratios for the respective components at Bethlehem showed that the values for most of the components increased at the HN treatment, with only grain yield, Ngrain and NUEYld at values less than one. The calculated NUE components NAEYld, NPE and NRE also showed non-additive gene action. At Vaalharts all the components showed additive gene action at both the LN and HN treatments, except for GP, NHI and NutEYld at the LN treatment. Also, in contrast to the response calculated at Bethlehem, the calculated NAEYld, NPE and NRE showed additive gene action. These differences in responses between the two environments can be attributed to the different growing conditions and N availability scenarios inducing the changes in response of agronomic and NUE components.

High broad-sense heritabilities were calculated for BM, grain yield, HM, TKM and HI at the LN and HN treatments at both localities. At Vaalharts the heritability value for GP was high at the HN treatment, and at Bethlehem at both the LN and HN treatments. Broad-sense heritability estimates improved at the HN treatment except for TKM compared to the LN treatment. The heritability values for the N uptake components, Ngrain, Ntotal and NHI were high, and were increased at the HN treatment. With the exception of the NutEYld component at the LN treatment at Vaalharts, the broad-sense heritability values of all the NUE components were high and increased by the HN treatment.

At Bethlehem the narrow-sense heritability value of TKM was high at both N treatments, and GP, TKM, NHI and NutEYld at the HN treatment. At Vaalharts high narrow-sense heritability values were found for HM, TKM at the LN treatment, as well as for NAEYld and NPE. All the agronomic and calculated components showed increased narrow-sense heritability values at the HN treatment. These responses indicate that the estimation of heritability of the studied components were improved when N were sufficiently available.

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CHAPTER 6

RECOMMENDATIONS

- The significant yield increases in wheat up to now have been the result of the introduction of the earliness and semi-dwarf genes into breeding programmes. However, to enhance grain yield in future, the possibilities of NUE components were investigated in this study. Results showed that significant variation exists between genotypes for the majority of NUE components.

  Higher broad and narrow sense heritabilities were found at the higher N application treatment for most of the NUE components. Of the NUE components measured, it was NupE% that was only phenotypicaly highly correlated with grain yield. In view of the significant variation between genotypes for NupE%, the relatively high broad sense heritability for NupE% and the strong phenotypic correlation with grain yield, it is recommended that wheat breeders rather concentrate on NupE% to enhance grain yields under optimal irrigation conditions. Because NupE% also links to the effectivity of N uptake by the root system, it is also recommended that the root system dynamics be included in further studies.

- This study has shown that the N treatments had significant effects on the GCA:SCA ratios of the measured components, with the exception of TKM. The additive gene action was significantly higher at the high N treatment. This was also the case for the NUE components NupE%, NUEYld and NutEYld. The practical implication is that the application of N increased the additive gene action proportionately. This increase was however not to the detriment of the SCA values but has shown greater expression of additive gene action at the high N treatment.

  Several possible explanations can be offered for this finding. One possibility is that certain additive genes are only activated at high N availability. Another possibility is that a higher level of inter-allelic interaction takes place at these high levels of N availability. This in turn can also increase the additive gene action proportionately. This study has shown that with the exception of TKM, and to a lesser extent HI, selection for grain yield increases should rather be under high N availability situations. The high levels of additive gene action at high N availability will increase the heritability and the response to selection. It is therefore recommended that for continued selection progress, selection for most of the characteristics should be conducted under high N fertility levels under irrigated conditions.

- The differences in climate, soils and crop rotations followed at the tested environments, influenced the residual soil mineral N and the NUE components of the cultivars, in combination with the N strategies followed. Results indicated that sufficient N fertilization is needed for high grain yields with an acceptable grain protein concentration, but that the effect of split applications of N during the growing season on the NUE components must be investigated further.

CHAPTER 7
SUMMARY

This study aimed at improving N fertilizer use efficiency by assessing the grain yield, N uptake, agronomic and physiological NUE components of irrigated wheat genotypes. The general and specific combining abilities of the genotypes for the NUE components were calculated, as well as the phenotypic correlations and broad and narrow sense heritability values.

Five South African irrigation cultivars were evaluated for differences in agronomic and NUE components to N management strategies at Riet River and Loskop irrigation schemes. The N treatments applied in 2000 and 2001 were a zero and optimum N application whereof the latter was split into four N management strategies. The two irrigation schemes had markedly different residual mineral N in the soil at planting in 2000 and 2001. Analyses of variance for grain yield, Ngrain, Ntotal, NHI, NAE, NRE and NPE showed that neither the main effect of cultivar and N treatments nor their interaction was consistent over the two localities over the two years tested. The effect of residual mineral N in the soil lead to low grain yields at the N0 treatment at Riet River in 2000, compared to 2001. Similarly at Loskop grain yield of the N0 treatments was lower in 2001 compared to 2000 when residual mineral N in the soil at planting was less.

In a second experiment, the NUE components of seven parental irrigation cultivars and their F_2-offspring were studied in 2004 at a cooler (Bethlehem) and a warmer (Vaalharts) irrigation environment. The genotypes were tested at two N treatments; a control (LN) and 180 kg N/ha (HN) applied. Agronomic characteristics, N uptake and NUE components were measured.

From the analysis of variance, the agronomic characteristics (BM, grain yield, HM, TKM and GP) showed significant genotypic variation. Harvest index, BM, HM and TKM showed no significant genotypic variation at the N treatment. The N uptake and NUE components showed significant genotypic variation with the exception of NutEYld. The HN treatment resulted in significant variation in Ngrain, Ntotal NHI, NUEYld and NutEYld. The HN treatment increased BM, grain yield and GP values, but reduced the HM, TKM, HI and NHI values of the genotypes. The NUE components NupE%, NUEYld and NutEYld were also reduced by the HN treatment.

Cultivars responded differently at the two N treatments in measured and calculated agronomic and NUE components. Olifants, Kariega and Marico showed good responses for the agronomic components at the HN treatment. Inia, SST 806, SST 822, Olifants, Kariega and Marico showed high values for NUE components. The crosses Olifants x Steenbras, SST 806 x SST 822, Marico x Steenbras, Olifants x SST 822 and Marico x SST 806 showed positive responses in the measured agronomical and NUE components.

The correlation coefficients were calculated to study the phenotypic resemblance between characteristics. The calculated correlation matrixes for the environments indicated positive correlation coefficients between several of the agronomic and calculated components. Biomass and grain yield was highly correlated with the NUE components, NupE%, NUEYld, Ngrain and Ntotal at both environments. Grain protein was negatively correlated to NutEYld, while NHI was positively correlated to this component. This points to the first order importance of grain yield production before grain protein under limiting N availability conditions. The correlation coefficients of components BM, grain yield, NPE, NRE and NUEYld increased at the HN treatment.

The effect of N treatments on the calculated GCA and SCA effects was studied from a diallel analysis. Significant GCA effects for the parental cultivars were found for the majority of the agronomic and NUE components at both N treatments. Significant SCA effects for the tested hybrids were also found at BM, grain yield, Ngrain, Ntotal, NupE%, NUEYld, NAEYld, PHE and NRE. The application of N fertilizer (LN versus HN treatments) affected the significance of the calculated combining abilities.

For the agronomic characteristics that were measured at Bethlehem, GCA effects for BM, HM, TKM, GP and HI were significant at the HN treatment. Significant GCA effects were found at the LN treatment for TKM and GP. The N uptake components Ngrain, Ntotal and NHI showed significant GCA effects at the HN treatment. For the NUE efficiency components significant GCA effects were calculated for NupE%, NUEYld and NutEYld at the HN treatment. No significant cultivar differences were found for the N uptake and NUE components at the LN treatment. For the agronomic components SST 822, Inia and Kariega generally had the highest GCA values. The cultivars Marico, Olifants, SST 806 and Inia showed the highest GCA values at the HN treatment for the agronomic, N uptake and NUE components.

At Vaalharts significant variability for GCA effects for the agronomic components BM, grain yield, HM, TKM and HI were found at both N treatments. For the N uptake components, significant GCA effects were calculated for Ngrain and Ntotal at both N treatments and for NHI at the HN treatment. Significant GCA effects were found for the NUE components NupE%, NUEYld at both N treatments and for NutEYld at the HN treatment. The cultivars Kariega, Olifants, Inia, Steenbras and SST 806 had the highest GCA values for the agronomic, N uptake and NUE components at the LN treatment. At the HN treatment Olifants, SST 806 and Inia had the highest GCA values for these components, as well as for the N uptake and NUE components.

The calculated SCA effects at Bethlehem were significant for BM, grain yield, Ngrain, Ntotal, NUEYld at both N treatments, and for NAEYld, NPE, NRE, HM and NupE% at the HN treatment. At Vaalharts significant SCA effects were calculated for BM, grain yield, Ngrain, Ntotal, NupE%, NUEYld at both N treatments and for NHI at the HN treatment.

The calculated GCA:SCA ratios for the respective components at Bethlehem showed that the values for most of the components increased at the HN treatment, with only grain yield, Ngrain and NUEYld at values less than one. The calculated NUE components NAEYld, NPE and NRE also showed non-additive gene action. At Vaalharts all the components showed additive gene action at both the LN and HN treatments, except for GP, NHI and NutEYld at the LN treatment. Also, in contrast to the response calculated at Bethlehem, the calculated NAEYld, NPE and NRE showed additive gene action. These differences in responses between the two environments can be attributed to the different growing conditions and N availability scenarios inducing the changes in response of agronomic and NUE components.

High broad-sense heritabilities were calculated for BM, grain yield, HM, TKM and HI at the LN and HN treatments at both environments. At Vaalharts the heritability value for GP was high at the HN treatment, and at Bethlehem at both the LN and HN treatments. Broad-sense heritability estimates improved at the HN treatment except for TKM compared to the LN treatment. The heritability values for the N uptake components, Ngrain, Ntotal and NHI were high, and were increased at the HN treatment. With the exception of the NutEYld component at the LN treatment at Vaalharts, the broad-sense heritability values of all the NUE components were high and increased by the HN treatment.

At Bethlehem the narrow-sense heritability value of TKM was high at both N treatments, and values of GP, NHI and NutEYld at the HN treatment. At Vaalharts high narrow-sense heritability values were found for HM, TKM, NAEYld and NPE at the LN treatment. All the agronomic characteristics and calculated components showed increased narrow-sense heritability values at the HN treatment. These responses indicate that the estimation of heritability of the studied components were improved when N were sufficiently available.

OPSOMMING

In die studie is die N verbruiksdoeltreffendheid (NUE) van koringcultivars onder besproeiing ondersoek deur graanopbrengs, N opname, agronomiese en fisiologiese NUE komponente te meet. De algemene (GCA) en spesifieke kombineervermoë (SCA) van die genotipes vir NUE komponente is bereken, asook die fenotipiese korrelasie koëffisiënte en oorerflikheidswaardes.

Vyf Suid Arikaanse besproeiingscultivars is evalueer vir verskille in agronomiese en NUE komponente in reaksie op N bestuurstrategieë by die Rietrivier en Loskop besproeiingskemas. Die N bestuursbehandelings het 'n geen (N0) en optimum N bemestingstoediening ingesluit, waarvan laasgenoemde verdeel is in vier N bestuursstrategieë, en is toegepas in 2000 en 2001. Die twee besproeiingsskemas het verskil in residuele minerale N in die grond met planttyd in 2000 and 2001. Die variansie analises vir graanopbrengs, Ngraan, Ntotaal, NHI, NAE, NRE en NPE toon dat die hoofeffekte cultivar en N behandeling en die interaksie tussen die hoofeffekte nie konstant reageer het by die twee besproeiingskemas oor die twee seisoene nie. Die effek van residuele minerale N in die grond het tot lae graanopbrengste by die N0 behandeling gelei by Rietrivier in 2000 in vergelyking met 2001. In ooreenstemming hiermee was die graanopbrengs van die N0 behandeling by Loskop met 'n verlaagde residuele minerale N met plant laer in 2001 in vergelyking met 2000.

In 'n tweede proef is die NUE komponente van sewe besproeiingscultivars en hulle F_2-kruisings getoets in 2004 in 'n koeler (Bethlehem) en 'n warmer besproeiingsomgewing (Vaalharts). Die genotipes is getoets by twee N behandelings; 'n kontrole (LN) en 180 kg N/ha (HN). Agronomiese eienskappe, N opname en NUE komponente is gemeet.

Betekenisvolle genotipiese variasie is gevind vir die agronomiese eienskappe (BM, graan opbrengs, HM, DKM en GP). Oesindeks, BM, HM en DKM toon geen betekenisvolle genotipiese variasie vir die N behandelings nie. Die N opname en NUE komponente toon betekenisvolle genotipiese variasie met die uitsondering van NutEYld. Die HN behandeling het betekenisvolle variasie in Ngraan, Ntotaal, NHI en NutEYld tot gevolg gehad. Die HN behandeling verhoog BM, graanopbrengs en GP, maar verlaag die HM, DKM, HI en NHI waardes van die genotipes. Die NUE komponente NupE%, NUEYld en NutEYld word ook verlaag deur die HN behandeling.

Die cultivars reageer verskillend in agronomiese en NUE komponente. Olifants, Kariega en Marico toon goeie reaksie in agronomiese eienskappe by die HN behandeling. Inia, SST 806, SST 822, Olifants, Kariega en Marico toon verhoogde NUE komponente. Die kruisings Olifants x Steenbras, SST 806 x SST 822, Marico x Steenbras, Olifants x SST 822 en Marico x SST 806 toon ook positiewe reaksie in agronomiese en NUE komponente.

Korrelasiekoëffisiënte is bereken om die fenotipiese ooreenstemmings tussen komponente te bepaal. Die berekende koëffisiënte vir die twee omgewings toon positiewe korrelasies tussen verskeie van die agronomiese en berekende komponente. Biomassa en graanopbrengs is hoogs gekorreleer met die NUE komponente, NupE%, NUEYld, Ngraan en Ntotaal. Graanproteïen is negatief gekorreleerd met NutEYld, terwyl die komponent positief met NHI gekorreleer is. Dit dui op die voorkeur van graanopbrengsvorming bo graanproteïen onder beperkte N beskikbaarheidstoestande. Die korrelasie koëffisiënte van die komponente BM, graanopbrengs, NPE, NRE en NUEYld is verhoog by die HN behandeling.

Die effek van N behandelings op die GCA en SCA waardes is met ‘n diallel-analise bestudeer. Betekenisvolle GCA effekte vir die ouer cultivars is gevind vir die meerderheid gemete agronomiese en NUE komponente by albei N behandelings. Betekenisvolle SCA effekte is ook gevind vir BM, graanopbrengs, Ngraan, Ntotaal, NupE%, NUEYld, NAEYld, PHE en NRE. Die toediening van N bemesting (LN versus HN behandelings) het die betekenisvolheid van die berekende effekte beïnvloed.

Die GCA effekte vir die agronomiese eienskappe BM, HM, TKM, GP en HI was betekenisvol by die HN behandeling op Bethlehem. Betekenisvolle GCA effekte vir DKM en GP is by die LN behandeling gevind. Die N opname komponente Ngraan, Ntotaal en NHI het betekenisvolle GCA effekte by die HN behandeling getoon. Betekenisvolle GCA effekte is bereken vir die NUE komponente NupE%, NUEYld en NutEYld by die HN behandeling. Geen betekenisvolle cultivarverskille is gevind vir N opname en NUE komponente by die LN behandeling nie. Die cultivars SST 822, Inia en Kariega het die hoogste GCA effekte vir die agronomiese eienskappe gehad. Die cultivars Marico, Olifants, SST 806 en Inia het die hoogste GCA gehad vir agronomiese, N opname en NUE komponente by die HN behandeling.

Betekenisvolle GCA effekte is vir die agronomiese eienskappe BM, graanopbrengs, HM, DKM en HI bereken vir albei N behandelings op Vaalharts. Betekenisvolle GCA effekte is ook bereken vir die N opname komponente Ngraan en Ntotaal vir albei N behandelings, en vir NHI by die HN behandeling. Die NUE komponente NupE% en NUEYld het betekenisvolle GCA effekte getoon by albei N behandelings, en vir NutEYld by die HN behandeling. Die cultivars Kariega, Olifants, Inia, Steenbras en SST 806 het die hoogste GCA waardes gehad vir die agronomiese, N opname en NUE komponente by die LN behandeling. Olifants, SST 806 en Inia het die hoogste GCA waardes gehad vir die agronomiese, N opname en NUE komponente by die HN behandeling.

Die berekende SCA effekte vir BM, graanopbrengs, Ngraan, Ntotaal, NUEYld was betekenisvol op Bethlehem by albei N behandelings, en vir NAEYld, NPE, NRE, HM en NupE% by die HN behandeling. Betekenisvolle SCA effekte is op Vaalharts bereken vir BM, graanopbrengs, Ngraan, Ntotaal, NupE% en NUEYld by albei N behandelings, en vir NHI by die HN behandeling.

Die verhouding GCA:SCA is bereken vir die gemete komponente en vir Bethlehem het die waardes van die meerderheid komponente toegeneem by die HN behandeling, met slegs graanopbrengs, Ngraan en NUEYld met waardes onder een. Die berekende NUE komponente NAEYld, NPE en NRE het ook nie-additiewe geenwerking getoon. Vir Vaalharts het al die komponente additiewe geenwerking getoon by die LN en HN behandelings, met die uitsonderings van GP, NHI en NutEYld by die LN behandeling. In teenstelling met die reaksie gemeet op Bethlehem, het die berekende NAEYld, NPE en NRE komponente additiewe geenwerking getoon. Die verskille tussen die twee omgewings kan toegeskryf word aan die verskille in groeitoestande en N beskikbaarheid wat gelei het tot verskillende reaksies in agronomiese en NUE komponente.

Hoë meer algemene oorerflikheidswaardes is bereken vir BM, graanopbrengs, HM, TKM en HI vir die LN en HN behandelings vir beide omgewings. Vir Vaalharts was die oorerflikheid hoog vir GP by die HN behandeling, en vir Bethlehem by beide die LN en HN behandelings. Die meer algemene oorerflikheidwaardes is verhoog by die HN behandelings behalwe vir DKM in vergelyking met die LN behandeling. Die algemene oorerflikheidswaardes vir die N opname komponente, Ngraan, Ntotaal en NHI was hoog, en is verder verhoog by die HN behandeling. Met die uitsondering van die NutEYld komponent by die LN behandeling op Vaalharts, was die algemene oorerfliheidswaardes van al die NUE komponente hoog en is verder verhoog by die HN behandeling.

Vir Bethlehem was die meer spesifieke oorerflikheidswaarde van DKM hoog by beide N behandelings, terwyl oorerflikheidswaardes vir GP, NHI en NutEYld hoog was by die HN behandeling. Vir Vaalharts is hoë meer spesifieke oorerflikheidswaardes bereken vir HM, DKM, NAEYld en NPE by die LN behandeling. Al die agronomiese en berekende komponente het verhoogde meer spesifieke oorerflikheidswaardes getoon by die HN behandeling. Hierdie reaksies dui daarop dat die skatting van oorerflikheid van die komponente wat ondersoek is verhoog is onder toestande waar N voldoende beskikbaar was.