YIELD AND QUALITY RESPONSE OF FOUR WHEAT CULTIVARS TO SOIL FERTILITY, PHOTOPERIOD AND TEMPERATURE

BY

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The nation with too much bread has many problems
the nation with too little bread has only one
problem

Fifth Century Byzantine Proverb

TO MY WONDERFUL MOTHER PENINAH YOGA
(MAA:NYAKWAR ONYANGO)

DAA (JI): ***Maureen Akinyi, Carole Achieng, June Amondi, Valary Adhiambo, Nickole Amollo, Fay Achieng, Penisoh Dimpho, Ian Rading and Wayne Aréche (Teddy, Fred and James Omondi)***

HERA MAR RUOTH YESU KENDE, JOKA MAMA!!!

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Last but not least, may the Almighty God bless the University of Pretoria as an excellent learning centre, its achievements and to continue prospering, and to the people of this beautiful nation of South Africa "SIMUNYE".

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DEGREE: PhD

ABSTRACT

The effects of soil nutrient status on the performance of four South African wheat genotypes were investigated in a long-term fertilization experiment. The objective was to quantify the effects of soil fertility on yield, yield components, grain nitrogen content, grain protein yield, grain protein content, flour yield and bread-making quality. The relative contribution of main stems and tillers, as well as the contribution of first, second and third kernels in the spikelets to grain yield and grain protein content were determined. The interactive effects between photoperiod, temperature and vernalization on grain yield, yield components and grain protein content were also quantified. Increasing soil fertility increased grain yield and most components of yield, grain nitrogen content, grain protein yield, aboveground biomass and harvest index, but depressed mean kernel mass. Significant interactions between cultivar and soil fertility were observed for grain yield, grain number, kernel mass, protein yield, biomass and harvest index, indicating differences in cultivar ability to produce yield and quality.

Within a cultivar, the main stem, first tiller and second tiller did not differ in mean grain protein content, indicating that late-maturing tillers do not affect the grain protein content of wheat.
Grain protein content, flour yield, loaf volume, water absorption and mixograph peak mixing time varied with soil fertility. The interaction between cultivar and soil fertility was significant for the above mentioned parameters with the exception of mixograph peak mixing time, indicating wheat genotypes differences in bread-making quality potential. The potential ability of wheat cultivar Kariega to produce higher grain yield, protein yield and loaf volume in the K and P limiting soil fertility situations deserve further investigation.

In a growth chamber study, the low temperature regimes and long photoperiod conditions resulted in the highest grain yield, number of grains, largest mean kernel size and highest grain protein content.

Key words: Bread-making quality, grain protein content, photoperiod, soil fertility, wheat yield and yield components.

CHAPTER 1

GENERAL INTRODUCTION

Grain yield and grain protein content are important in the production and marketing of wheat (*Triticum aestivum* L.). Recent changes in the balance of supply and demand as a result of the new global economy mean that growers must produce grain that matches demand more closely and reliably (Moss, 1973; Laubscher, 1981; Van Lill & Purchase, 1994). In South Africa wheat is grown under irrigation and rainfed conditions, varying soil fertility situations and a wide range of climatic conditions. Breeding programmes are aimed at developing high yielding cultivars with appropriate quality characteristics (Laubscher, 1981; Purchase, Botha, Maritz & Van Tonder, 1992; Van Lill & Purchase, 1994). The factors determining wheat yield, grain protein content and bread-making quality have been investigated by many researchers (Terman, Ramig, Dreier & Olson 1969; Takeda & Frey, 1979; Laubscher, 1981; Ciha, 1984; Fischer, 1989; Randall, Manley, McGill & Taylor, 1993). These studies indicate that when soil moisture and weather conditions are favourable the variation in wheat yield, grain protein content and bread-making quality are determined by genotype and soil fertility status.

The breeding and selection for higher grain yield, improved grain protein content and bread-making quality is often a lengthy and costly process. Normally, it takes about 14 to 15 years to produce, multiply and release a new wheat variety, while the life span of a cultivar may be only 5 to 6 years (Balla, 1986; Bell, 1987).

In this investigation interaction effects between cultivar and soil fertility on yield, grain protein content and bread-making quality were studied in a long-term fertilization experiment. The results presented and discussed were obtained during a two year (1995 and 1996) field study and in growth chambers (1997). The 1995 and 1996 results were similar, and for economy of resources only 1995 results are presented, except where otherwise indicated. The 1996 data is available, and if required, may be obtained on request from the Head, Department of Plant Production and Soil Science, University of Pretoria, Pretoria 0002, South Africa.

1.1 LONG-TERM FERTILIZATION EXPERIMENTS

A long-term field experiment is considered to be one in which the original treatments are repeated on the same plots year after year, for many years (Frye & Thomas, 1991; Mitchell, Westerman, Brown & Peck, 1991). If the treatments are changed every few years, all that occurs is a series of short-term experiments conducted on the same site for a long period of time. Long-term experiments are essential for obtaining information on the long-term sustainability of agricultural systems Leigh & Johnston (1994). They play an essential role in understanding the complex interaction of plants, soils, pests, climate and management problems, and their effects on sustainable crop production. The classical experiment at Rothamsted in England (Jenkinson, 1991) is a typical example. Four of America's oldest, continuous agronomic research trials, the Illinois "Morrow Plots" (1876), Missouri's "Sanborn Field" (1888), Oklahoma's "Magruder Plots" (1892) and Alabama's "Old Rotation" (1896) have been reviewed in detail by Mitchell et al. (1991). These studies show that long-term crop production can be sustained and improved in different regions and on different soils.

A fertilizer and irrigation experiment on the Experimental Farm of the University of Pretoria was established in 1939 and is one of the oldest long-term experiments in southern Africa (Nel, Barnard, Steynberg, De Beer & Groeneveld, 1996). Studies have been published on facets of this trial. Nel (1972) reported on traits in maize grain yields during the first 32 years of the trial; Verwey (1974) on growth and yield of maize at different fertilizer and water levels in the 1972-1973 growing season; Stoch (1983) on the variability in certain individual treatments over the first 28 years of the trial; Steynberg (1986) on growth, development and water use efficiency of maize in 1983-1984 and 1984-1985 seasons; Annandale, Hammes & Nel (1987) on the effect of soil fertility on the vegetative growth, yield and water use of wheat and Nel *et al*. (1996) on trends in maize grain yields in a long-term fertilization trial.

After more than 50 years of different fertilization treatments, the long-term trial at the University of Pretoria offers a unique opportunity to study the effect of soil fertility on growth, yield and quality of wheat on one site under the same climatic conditions. The range of divergent soil fertility conditions available also presents a rare opportunity to investigate cultivar x soil fertility interactions. This valuable site was therefore utilized for the field experiments reported in this thesis. Publications emanating from this includes Metho, Hammes, De Beer & Groeneveld (1997) on the interaction between cultivar and soil fertility on grain yield, yield components and grain nitrogen content of wheat; Metho, Hammes & Beyers (1998) on the effect of soil fertility on the contribution of main stem, tillers, kernel position to grain yield and grain protein content of wheat and Metho, Taylor, Hammes & Randall (1999) on the effects of cultivar and soil fertility on grain protein yield, grain protein content, flour yield and bread-making quality of wheat.

1.2 INTERACTION EFFECTS BETWEEN SOIL FERTILITY AND CROP CULTIVARS

High grain yield, grain nitrogen content, protein yield and grain protein content in wheat can be associated with relatively high and balanced soil fertility regimes. Nutrient imbalances have been reported to cause drastic reduction in grain yield and quality both in field and growth chamber conditions (Laubscher, 1981; Fischer, 1989).

Many researchers have reported that soil variability has a greater impact on crop yield and quality than other production factors (Liang, Heyne & Walker, 1966; McMullan, McVetty & Urquhart**,** 1988). Carr, Jacobsen, Carlson & Nielson (1992) reported that grain yield and protein content of a barley cultivar and a wheat cultivar differed across three soils, and observed soil fertility x cultivar interactions for test weight and grain protein content. Other workers have reported significant variety x location and variety x year x environmental interactions (Liang, *et al*., 1966; Ciha, 1984; Baenziger, Stephen, Clements, McIntosh, Yamazaki, Starling, Sammons & Johnson, 1985; Carr, *et al.,* 1992). The significant soil fertility and cultivar interactions clearly indicate that wheat genotypes react differently to different soil fertility situations. Published research data show that variations in soil nutrient status can result in grain yield and grain quality differences, often in the same field (Laubscher, 1981; McMullan *et al*., 1988; Carr *et al*., 1992). Such results show that breeding and cultivar evaluation should place more emphasis on soil fertility and crop genotype interactions for improved yield and quality.

1.3 YIELD COMPONENTS

Cereal yields vary as a result of combined effects of ears per unit area, grains per ear and kernel mass. These yield components vary widely with cultivar, moisture supply, soil fertility level and other growth limiting factors. Increases in the various yield components as a result of breeding, increased availability of nitrogen, or improved soil fertility status, have been reported by many researchers (Donald, 1968; Nass, 1973; Darwinkel, 1978; Nerson, 1980; Briggs, 1991).

The relative contribution of main stems and tillers as well as the relative contribution of first, second and third kernels in the spikelet, to grain yield and grain protein content, are seldom quantified. This may be important in South Africa where late maturing tillers are reportedly affecting grain yield and wheat quality (Wheat Board Technical Reports, 1990/95). Therefore, the hypothesis that tillers affect the quality of grain to a greater degree than their contribution to grain yield was tested. This kind of data is rarely available, but may be be useful in management strategies to improve yield and quality for different environments.

1.4 GRAIN PROTEIN CONTENT AND QUALITY

Grain protein content has been found to increase with the amount of applied nitrogen whether or not a yield increase resulted (Finney, Meyer, Smith & Fryer, 1957; Schleuber & Tucker, 1959; Terman, *et al*., 1969; Laubscher, 1981). Grain protein content affects the flour yield and bread-making quality of wheat. Grain protein content is genetically and environmentally controlled, and may vary with cultivar, soil fertility, location and climate. Genotype and environment interaction plays a major role in determining grain protein content level.
The interface between actual field nutrient status, cultivar productivity and product quality is important for South Africa where the price of wheat grain is determined on the basis of grain protein content and bread-making quality. For a specific cultivar an increase in grain protein content normally results in increases in water absorption and loaf volume (Finney & Barmore, 1948; Tipples & Kilborn, 1974; Tipples,Dubetz & Irvine, 1977). Wheat yield and grain protein content have been increased through breeding and selection as independent traits (Pendleton & Dungan, 1960; Terman *et al*., 1969; Jenner, Ugalde & Aspinall, 1991).

Improved grain protein content and higher yield from crosses between high yielding and good quality wheat genotypes have been reported (Borghi, Corbellini, Cattaneo, Fornasari & Zucchelli 1986; Perenzin Pogna & Borghi, 1992). Payne (1987) and Randall, *et al*. (1993) have reported a significant correlation of certain high molecular weight subunits of glutenin

(HMW-GS) with end-use quality of wheat, specifically dough strength. These results indicate that greater precision may be introduced into selection for bread-making quality in the future, but the relationship between the quality and quantity of high molecular weight subunits of glutenin and end-use quality properties still requires detailed investigation.

1.5 PHOTOPERIOD, TEMPERATURE AND VERNALIZATION

In South Africa wheat is grown under divergent climatic conditions varying from cool short days to warm long days. This affects yield and grain quality. Several studies on the effects of photoperiod, temperature and vernalization of wheat have been reported (Nel & Small, 1969; Wardlaw, 1970; Joubert & Laubscher, 1974; Warrington, Dunstone & Green, 1977; Human, Nel, Hammes & Beyers, 1981), but none of these reported on the interactive effects between photoperiod, temperature and vernalization on grain yield and grain protein content. Understanding the interactive effects of photoperiod, temperature and vernalization on cultivar grain yield, its components and grain protein content may contribute towards wheat yield, quality and regional adaptability.

1.6 EXPERIMENTAL OBJECTIVES

The objectives of this investigation were:

1. To quantify the effect of soil nutrient status on the grain yield, components of yield, and grain protein content of four South African spring wheat cultivars, thus to test the hypothesis that wheat cultivars differ in their potential to produce yield and quality under varying soil fertility situations.
2. To determine whether main stems, first tillers and second tillers differ in grain protein content, and thus to test the hypothesis that tillers affect the quality of grain to a greater degree than their contribution to grain yield.
3. To determine kernel size distribution in the spikelets of four wheat cultivars.
4. To determine whether grain protein percentage differ between kernels at different positions on the spikelet.
5. To determine the harvest index of main stems, first and second tillers of four South African wheat cultivars under different soil fertility regimes.

6. To quantify the effects of six soil fertility regimes on grain protein yield, grain protein content, flour yield and bread-making quality characteristics of different cultivars cultivars.
7. To quantify the effects of photoperiod and temperature on grain yield, yield components and grain protein content of vernalized and unvernalized wheat in growth chambers.

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CHAPTER 2

INTERACTION BETWEEN CULTIVAR AND SOIL FERTILITY ON GRAIN YIELD, YIELD COMPONENTS AND GRAIN NITROGEN CONTENT OF WHEAT

2.1 ABSTRACT

The effect of soil nutrient status on the performance of four wheat cultivars was studied in a long-term field experiment at the University of Pretoria. The objective was to quantify the effect of soil nutrient status on yield, yield components and grain quality characteristics, using a split-plot design in a randomized complete block, replicated four times. The cultivar Carina produced the highest grain yield and grain nitrogen content averaging 6343 kg ha^{-1} (3.58%N) while SST 86, Kariega and Inia did not differ significantly but ranged from 3903 kg ha^{-1} (2.47%N), 4447 kg ha^{-1} (2.49%N) to 4484 kg ha^{-1} (2.58%N) respectively. Increasing soil fertility increased grain yield, grain number, spikelet number, grains per spike, grains per spikelet, grain nitrogen, biomass and harvest index, but depressed mean kernel mass. Significant interactions between cultivar and soil fertility were observed for grain yield, grain number, biomass, harvest index and mean kernel mass. The ability of the cultivar Kariega to produce higher grain yield in the K limiting soil fertility situation deserves detailed investigation. It is concluded that wheat cultivars differ in their potential to utilize limited soil nutrients to produce yield and quality.

Key words: Soil fertility, *Triticum aestivum*, wheat genotypes, yield components.

Publications and conference presentations based on this study:

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2.2 INTRODUCTION

Major objectives in wheat (*Triticum aestivum* L.) cultivar development programmes are increased grain yield, improved grain protein concentration and quality. Improvement of grain yield and protein content through direct selection is difficult because of the well-documented negative association (Pendleton & Dungan, 1960; Terman, Ramig, Dreier & Olson, 1969).

Several authors suggest that improved protein content and higher yield can be obtained from crosses between high-yielding and good quality wheat genotypes (Baligar & Bennet, 1986; Borghi, Corbellini, Cattaneo, Fornasari & Zucchelli, 1986; Perenzin, Pogna & Borghi, 1992), improved soil nutrient concentrations (Laubscher, 1981; McMullan, McVetty & Urquhart, 1988; Randall, Freney, Smith, Moss, Wrigley & Gallaby, 1990) and fertilizer management (Dubetz, 1972; Corino, Boggini, Bonali & Borghi, 1975; Pearson, Rosielle & Boyd, 1981; O'Brien & Ronalds, 1987; Fischer, 1989). Efforts to simultaneously improve grain yield and protein concentration have explored parameters such as total dry matter accumulation and partitioning (Takeda & Frey, 1979), harvest index (Jennings & Shibles, 1968; Donald & Hamblin, 1976), and total nitrogen content (Austin, Ford, Edrich & Blackwell, 1977; Desai & Bathia, 1978; Cox, Qualset & Rains, 1985a).

Grain nitrogen concentration is dependent on grain carbohydrate content (Cox, Qualset & Rains, 1985b; Strong, 1986; McMullan, McVetty & Urquart, 1988), and several studies have demonstrated that genetic variability exists for grain nitrogen content (Johnson, Schmidt & Mattern, -1968; Desai & Bathia, 1978; Cox, Qualset & Rains, 1985b). Therefore, important factors for producing wheat with high yield and protein content when soil moisture and weather conditions are favourable, are genotype and soil fertility.

Fertilization, particularly of nitrogen and phosphorus, is a major input in wheat yield and quality (Fischer, 1979, 1989; Bacon, 1995). Reports on the efficiency of nutrient use, and of wheat genotypes able to produce good yields in less favourable soil nutrient supply conditions, have been published (Arnon, 1974; Fischer, O'Brien & Quail, 1989). Wheat genotypes with the potential to utilize limited soil nutrients may be important to South Africa and other areas with relatively infertile soils.

Long-term trials are an important way of obtaining information on sustainability of agricultural systems (Nel, Barnard, Steynberg, De Beer & Groeneveld, 1996). This has been demonstrated at

Rothamsted (Johnston & Mattingly, 1976; Jenkinson, 1991), University of Illinois (Mitchell, Westerman, Brown & Peck, 1991), and in Australia and India (Leigh & Johnston, 1994). A long-term fertilization experiment, initiated in 1939 at the University of Pretoria, provided a good opportunity for studying wheat cultivar performance over a wide range of soil fertility.

The objectives of this study were: (i) to quantify the effects of varying soil nutrient regimes on yield, yield components and grain quality characteristics, and (ii) to test the hypothesis that wheat cultivars differ in their potential to produce yield and quality under varying soil fertility situations.

2.3 MATERIALS AND METHODS

Site, Soil and Experimental Design

A long-term fertilization experiment located at Hatfield Farm, University of Pretoria (Lat. 25^o 45'S, Long. 28^o 16'E, elevation 1372 masl) was utilized for this study. The soil is classified as mesotrophic, luvic dark red brown soil of the Hutton form (Soil Classification Group, 1991) and by the USDA Soil Taxonomy System (Soil Survey Staff, 1990), as loamy, mixed, thermic Rhodic Kaundidalf (Nel, Barnard, Steynberg, De Beer & Groenveld, 1996).

Monthly rainfall, evaporation and mean minimum and maximum temperatures for the 1995 winter season are shown in Figure 2.1 (Appendix Figure 9.A1). Six soil fertility treatment combinations (NPKM NPK PK NP NK & Control) were selected from the long-term fertilization experiment started in 1939.

The long-term 2^5 factorial experiment comprising two levels of nitrogen, phosphorus, potassium, manure and water was laid out according to a randomized complete block design replicated four times. In this experiment spring wheat is rotated with soybean (*Glycine max*. L.) in summer, with the fertilizer applied to the wheat. In our experiment the six selected fertility plots were the main plots and was split to accommodate four local wheat cultivars Inia, Carina, Kariega and SST 86 as the sub-plots. The cultivars were planted in unrandomized strips on the sub-plots. Main plot size was 8.2 m by 6.3 m and the sub-plot size 1.2 m by 6.3 m. Details of treatments are given in Table 2.1.

Soil analysis data is presented in Table 2.2 for the 0-200 mm soil layer for the selected treatments. This reflects the actual site pH and fertility regimes representing the effect of differential fertilization over more than 50 years.

Cultural practices

The wheat was planted on 15 and 16 May 1995 at a 300 mm inter-row spacing. Plant populations ranged from 365 plants m^{-2} for Inia, 284 for Carina, 232 for Kariega and 244 for SST 86 depending on seed size and viability. The seedbed was prepared using a rotovator while planting was done manually. Throughout the growing season water was supplied by overhead sprinkler irrigation amounting to a total of 450 mm. Due to its longer growing period Carina received an additional 120 mm. Standard disease and pest control measures were applied. Harvesting was done by hand and after oven drying at 60 ^{o}C for 48 hr, the samples were threshed with a portable thresher to obtain grain yield.

Data recorded

Plants from 1 m^2 area, as well as an additional sample of 5-plants, were harvested on five occasions from emergence to maturity from each plot. Total above-ground biomass (g m^{-2}), grain yield (g m^{-2}), grain number m^{-2}, spikes m^{-2}, 1000-grain mass, harvest index and final crop height (mm) were determined from the 1 m^2 bulk samples. Number of tillers per plant, spikelets per spike and grains per spike were determined from the additional 5-plant samples. To cause minimum interference with the rotation practice only treatments NPKM, NPK and 'O' Control were retained for determination of grain yield in the case of the late maturing cultivar Carina. Grain nitrogen content and straw nitrogen content at final harvest were determined according to a standard Kjeldhal procedure (AACC, 1983).

Statistical analyses

Data were analysed by analysis of variance using SAS/STAT (SAS Institute Inc. Cary, NC., USA 1989 Copyright). Differences at the $P \leq 0.05$ level of significance are reported. Means were separated using Tukey's range test. Bartlett's test for homogeneity of the variance was performed on main and sub-plot variances. Tests for heterogeneity of variances for all characteristics measured were done and probabilities calculated according to Steel & Torrie (1980).

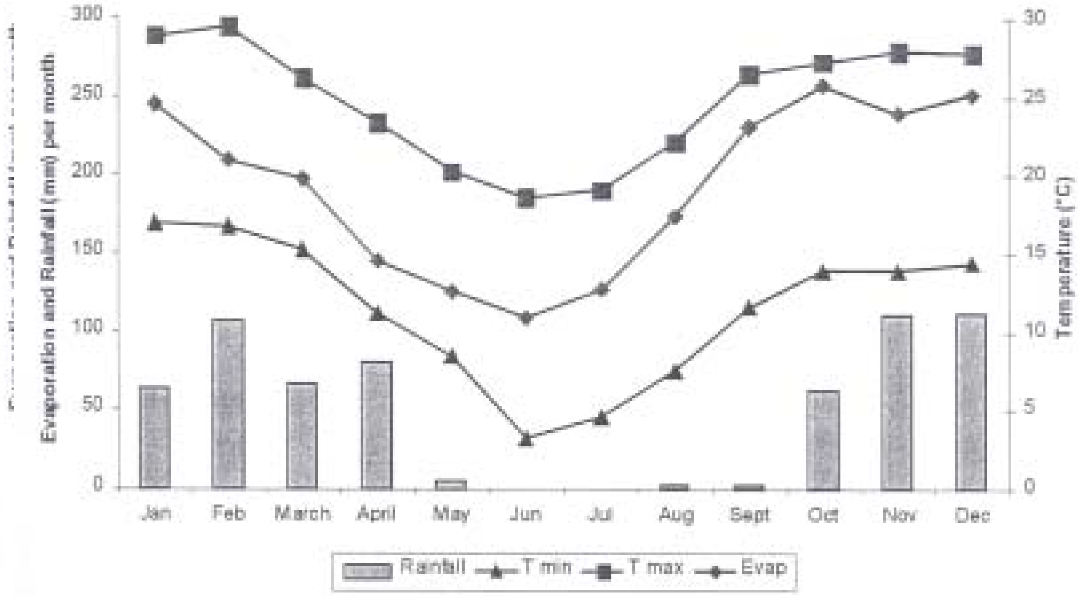

FIGURE 2.1 Metereological data for Hatfield showing mean max and min temperatures, evaporation and rainfall (mm), 1995.

Table 2.1 Details of experiment conducted on four local wheat cultivars grown under irrigation at Hatfield, Experimental Farm, University of Pretoria

Practices 1995	
Crop rotation	Wheat grown during the winter period may to October and soybean (*Glycine Max L. Mervil cv. Usutu* from November to March, except the year prior to 1995 when the plots were fallowed.
Planting date	15 and 16 May (using Planet Junior, planter USA).
Wheat cultivars	Inia – Pureline, semi-dwarf spring type released in 1966 by the Department of Agriculture. Carina – Hybrid, semi-dwarf winter type released in 1989 by Carnia Kariega – Semi-dwarf spring type released in 1993 by the Small Grain Institute. SST 86 – Dwarf spring type released in 1987 by Sensako.
Seeding rate (Based on seed size)	Inia – 100 kg ha^{-1} Carina – 70 kg ha^{-1} Kariega – 100 kg ha^{-1} SST 86 – 150 kg ha^{-1}
Nutrient treatments	N – 100 kg N ha^{-1} (KAN 28%) P – 70 kg P ha^{-1} (Single superphosphate, 8.3%) K – 50 kg K ha^{-1} (Potassium chloride 50%) M – 15 tons ha^{-1} (Farmyard manure) Lime – 180 kg ha^{-1} (Agricultural lime, ($Ca(OH)_2 + MgSO_4$)
Diseases & Pests	No major disease was recorded, however, Loose smut (*Ustilago tritici*) was controlled by removing infected plants. Harvester termites (*Hodotermes sp*) were controlled by parathion (Folimat, WP) at 1,5 kg ha^{-1}. Bird damage limited by using protective netting.
Maturity period	Inia and SST 86 reached physiological maturity on 16 October, Kariega on 23 October and Carina by 16 November.

Table 2.2 Soil analysis (0 – 200 mm) for the six selected fertility treatments for experimental site, 1995

Treatment	PH (H₂O)	Bray 2 P mg kg^{-1}	K mg kg^{-1}	Ca mg kg^{-1}	Mg mg kg^{-1}	Na mg kg^{-1}
NPKM	5.8	109	120	865	225	26
NPK	5.4	63	66	553	180	27
PK	6.0	43	92	606	196	25
NP	5.1	37	21	529	199	25
NK	5.2	1.8	81	493	140	26
"O" Control	6.1	1.7	22	541	239	25
LSD_T						
$P_{\leq 0.05}$	0.4	20.6	30.3	49	45	2.4
CV %	3.7	46.5	49.1	23.4	20.1	2.8

Correlation analysis was performed to determine the relationship between grain yield and yield components.

2.4 RESULTS AND DISCUSSION

The main effects of genotype and soil fertility on yield, yield components and grain nitrogen content are summarized in Tables 2.3 and 2.4. Significant cultivar x soil fertility interactions were observed for grain yield, grain number, grain mass, aboveground biomass, crop height and harvest index, and are illustrated in Figures 2.2.

Grain yield

Under the experimental conditions Carina produced the highest yield (6343 kg ha^{-1}) while for SST 86, Kariega and Inia the grain yield ranged from 3903 to 4484 kg ha^{-1}, but did not differ significantly (Table 2.3). These results are not necessarily an indication that Carina is a suitable cultivar for commercial production in the Gauteng Province of South Africa. The extremely long growing period of this cultivar (more than 30 days longer than the other cultivars) is a distinct disadvantage despite its good yield (Appendix Figure 9.A12).

The control plots which received no fertilization or manure since 1939 produced an average yield of 1300 kg ha^{-1}, showing sustainable yield without fertilization. Jenkinson (1991) reported an average yield of 1400 kg ha^{-1} from unfertilized wheat plots at the Rothamsted classical experiments.

Grain yield increased with increasing soil fertility (Table 2.3). The NPKM, NPK and PK treatments did not differ, but yielded more than the NP treatment. The NK and 'O' Control treatments resulted in the lowest yields. Residual nitrogen from the soybean (*Glycine max.*) rotation crop probably explains the good yield obtained from the PK treatment. The NP treatment, which over the years resulted in a K-deficient soil, produced higher grain yield than NK treatment which is associated with low soil P.

The cultivar x soil fertility interaction on grain yield is illustrated in Figure 2.2(A), showing no differences in the performances of the cultivars at the 'O' Control, NK, PK and NPKM treatments. In general the cultivars performed similarly as yield increased with increasing soil fertility. The significant interaction between cultivar and soil fertility was mainly due to Kariega out-yielding SST 86 in the treatment where K was in low supply (NP treatment). This may be an indication of the ability of cultivar Kariega to obtain potassium more efficiently from deeper soil layers, and is an aspect deserving further attention.

These results are consistent with the findings of Carr, Carlson, Jacobsen, Nielsen & Skogley (1991) and Carr, Jacobsen, Carlson & Nielsen (1992) whom reported significant soil x cultivar interactions for grain yield, test weight and grain protein of both spring barley (*Hordeum sp.*) and wheat. Liang, Heyne & Walter (1966) reported that soil variation may explain environmental x cultivar interactions for several cultivars of winter wheat and winter barley. Lee & Spillane (1970) also reported that both cultivar and fertilization management must be considered for optimum crop yield and quality in fields with different soils. However, absence of significant cultivar x soil fertility interactions have also been reported (Strong, 1986).

TABLE 2.3 Effect of cultivar and soil fertility on grain yield, spike number, spikelets per spike, grains per spike, grain number, grain mass and grain nitrogen content

Treatment	Grain yield (kg ha^{-1})	Spikes (m^{-2})	Spikelets per spike	Grains per spike	Grain number (m^{-2})	1000 Grain mass (g)	Grain N content (%)
Cultivar [1]							
SST 86	3 903	349	16.9	29.3	11 650	36.2	2.47
Inia	4 484	403	16.7	27.6	12 342	36.9	2.53
Kariega	4 447	454	18.2	29.9	14 821	33.4	2.49
Carina	6 343	508	20.1	42.8	23 956	27.4	3.58
LSD_T							
$P_{\leq 0.05}$	1 031	100	2.0	10.5	3 587	2.1	0.98
Fertility [2]							
NPKM	6 163	511	19.6	38.0	19 266	33.9	2.78
NPK	5 590	477	19.2	35.2	16 629	35.1	2.58
PK	4 896	394	18.9	31.8	12 424	39.5	2.16
NP	3 332	475	17.6	24.8	11 903	27.8	2.31
NK	1 300	260	14.7	13.7	3 523	36.6	2.39
'O' Control	1 081	219	13.0	13.6	2 918	37.4	2.13
LSD_T							
$P_{\leq 0.05}$	1 480	168	1.9	11.9	3 880	3.9	0.30
CV %	18.3	21.5	9.7	21.7	16.6	5.8	5.4

(1) Cultivar data based on treatments NPKM, NPK and 'O' only.
(2) Fertility data excludes Carina.

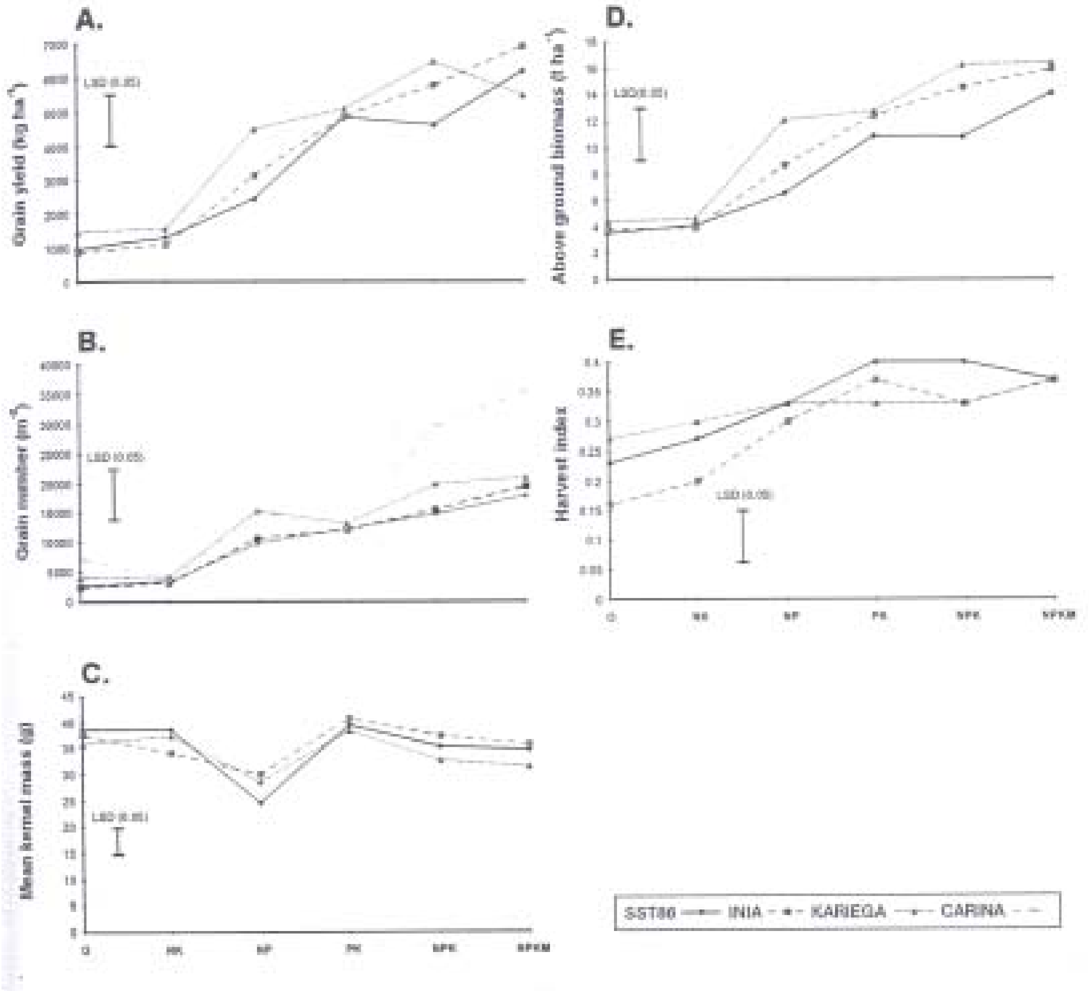

FIGURE 2.2 Interaction between cultivar and soil fertility on grain yield (A), grain number (B), mean grain mass (C), biomass (D) and harvest index (E).

Yield components

In general Carina produced significantly more spikes per unit area, more spikelets per spike and more grains per spike than SST 86. Number of spikes per unit area, spikelets per spike and grains per spike determine grain number per m^2. Regardless of cultivar differences in tillering and final spike number, our data are consistent with many reports which have demonstrated the need for higher spike densities to produce higher yields (Scott, Dougherty & Langer, 1975; Hampton, McCloy & McMillan, 1981). Bullman & Hunt (1986) found that grain yield of wheat was linearly related to spike number.

Studies by Darwinkel (1978; 1983) and Nerson (1980) have shown that although grain number per spike and kernel mass can compensate somewhat for deficient spike populations, they cannot adequately make up lost yield potential. When spike densities are low (as in '0' Control and NK treatments), grain number per spike and kernel mass cannot compensate sufficiently for the low number of spikes to make up for lost yields (Nerson, 1980).

Generally, increased soil fertility increased number of spikes per m^2, spikelets per spike, grains per spike and hence grains per m^2. The NP, PK, NPK and NPKM treatments did not differ in spikes per m^2 and spikelets per spike, with the '0' and NK treatments significantly lower. Treatments NPK and NPKM produced the highest number of kernels per spike, with '0' (control), NK and NP treatments lowest. The PK treatment was intermediate in grains per spike (Table 2.3).

The interaction between cultivar x soil fertility was not significant for spikes per m^2, spikelets per spike and grains per spike. However, cultivar x soil fertility was significant for grain number per m^2, due to Carina producing more grains than SST 86, Inia and Kariega in the NPK and NPKM treatments (see Figure 2.2).

Kernel mass varied with cultivar, though not statistically different, with Carina producing the smallest kernels, as can be seen from the 1000 grain mass in Table 2.3. Kariega produced intermediate kernels, while SST 86 and Inia had larger kernels. At higher soil fertility (NPKM treatment) smaller kernels were produced, probably because of poor grain-filling in response to competition due to the large sink-size. The PK treatment resulted in the largest mean kernel mass and the NP treatment had the smallest kernels (Table 2.3). The interaction between cultivar and soil fertility was significant for kernel mass due to the fact that on plots low in P (NK treatment) SST 86 produced larger kernels than Inia, while on K-deficient plots (NP treatment) the cultivar Inia had larger kernels than SST 86 (Figure 2.2). Although the NK and 'O'. Control treatments had relatively large kernels, these plots produced the lowest yields, due to low grain number per unit area.

Our data indicate that the magnitude of compensation between yield components was relatively small, a decrease in number of spikes per m^2 was not adequately compensated for by either grains per spike or kernel mass. Each yield component varied independently of the others and hence, the findings are in agreement with those reported by Gallagher & Biscoe (1978) and Hay & Walker (1989).

While no single yield component was predominant in determining yield, number of grains per unit area was positively correlated (r = 0.95) with yield. Evans (1987) reported that components of yield are interdependent to a greater or lesser degree, and that greater number of spikes per unit area is counteracted by a smaller number of grains per spike.

Grain nitrogen

The cultivars differed in grain nitrogen content with Carina having the highest percentage (Table 2.3; Appendix Table 9.A2). SST 86, Inia and Kariega did not differ in grain nitrogen content.

Generally grain nitrogen increased with increasing soil fertility, with the NPK and NPKM treatments significantly higher than the PK and Control treatments. The interaction between cultivar x soil fertility for grain nitrogen was not significant. Benzian & Lane (1981) reported a consistent linear relationship between grain nitrogen concentration and grain yield of wheat to increasing fertilizer N. Many authors have reported fertilization strategies in which split N application between planting and flowering increased grain nitrogen content (Finney, Meyer, Smith & Fryer, 1957; Langer & Liew, 1973; Strong, 1981). Strong (1986) reported no significant interaction between N and growth application stage in wheat.

These results are in agreement with our findings showing grain yield and grain nitrogen content varied with cultivar and only improved in balanced soil fertility treatments (NPK and NPKM treatments) but were reduced in less favourable soil fertility situations (PK, NP, NK and '0'(Control) treatments). Benzian & Lane (1979) found that grain yield, nitrogen concentration of the grain and nitrogen yield varied widely from site to site and from year to year. The proportion of total amount of nitrogen present in the grains, the nitrogen harvest index, centres around 0.78 – 0.82 under optimum conditions (Spiertz & De Vos, 1983) and was comparable with our findings (Appendix Table 9.A9).

Biomass, harvest index and crop height

The cultivars differed in biomass production, harvest index and final crop height (Table 2.4). Carina produced the largest biomass, highest harvest index and was the tallest, while SST 86 had the lowest biomass and was the shortest. Carina, SST 86 and Kariega did not differ in harvest index while Inia had the lowest (Table 2.4).

In general biomass, harvest index and crop height increased with increasing soil fertility (Table 2.4). The NPK and NPKM treatments did not differ but produced the largest biomass. The PK and NP treatments were intermediate, while the NK and 'O' (Control) treatments were the lowest. Treatments PK, NPK and NPKM had the highest harvest index and tallest crop height, while NP, NK and 'O' Control treatments had significantly lower harvest indices and shorter crop heights (Table 2.4; Appendix Table 9.A4).

The cultivar x soil fertility interaction was significant for biomass and harvest index, as illustrated in Figure 2.2. Yield increases have been attributed to genotypic improvement of dry matter distribution as has been found by a comparison of old and modern wheat and barley varieties (Austin, Bingham, Blackwell, Evans, Ford, Morgan & Taylor, 1980). High N dressings resulted in increased biomass yield at anthesis and in enhanced N contents of the vegetative parts of the crop and grain yield (Spiertz & De Vos, 1983). Further increase of the amount of N associated with high soil fertility may result in adverse effects such as lodging.

TABLE 2.4 Effect of cultivar and soil fertility on biomass, harvest index and crop height at final harvest

Treatment		Biomass ($t\ ha^{-1}$)	Harvest index	Crop height (mm)
Cultivar [(1)]				
	SST 86	9.3	0.33	708
	Inia	11.4	0.29	943
	Kariega	12.3	0.32	900
	Carina	15.6	0.36	1 018
	LSD_T			
	$P_{\leq 0.05}$	1.5	0.01	64
Fertility [(2)]				
	NPKM	15.5	0.37	950
	NPK	13.8	0.36	919
	PK	12.0	0.37	886
	NP	9.1	0.32	736
	NK	4.2	0.26	692
	'O' Control	3.9	0.22	682
LSD_T				
$P_{\leq 0.05}$		3.3	0.11	75.6
CV %		16.0	16.2	6.0

Significant at the P≤ 0.05 level.

[(1)] **Cultivar data based on treatments NPKM, NPK and O only.**

[(2)] **Fertility data excludes Carina.**

2.5 CONCLUSIONS

Wheat cultivars are often recommended for relatively large geographic areas encompassing a range of varying soil fertility situations. Edaphic variation in chemical or physical properties can result in large differences in grain yield and grain nitrogen content and hence, grain quality. Research has also indicated that relative performance of wheat cultivars may change across contrasting soils in a field (Ciha, 1984; Carr *et al*., 1992).

Our data, from a long-term fertilization trial which has been maintained under differential fertilization for more than fifty years, indicate that differences in grain yield and quality occurred mainly in plots low in K. The cultivars generally reacted similarly across the range of soil fertility regimes, however, significant cultivar x soil fertility interactions were observed for grain yield, grain number, mean kernel mass, biomass and harvest index, showing differential cultivar performance.

These results show that breeding and cultivar evaluation should continue placing more emphasis on soil fertility in order to understand how cultivars react to less favourable soil fertility situations to produce yield and quality.

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CHAPTER 3

THE CONTRIBUTION OF MAIN STEM, TILLERS AND KERNEL POSITION TO GRAIN YIELD AND GRAIN PROTEIN CONTENT OF WHEAT

3.1 ABSTRACT

The relative contribution of main stems and tillers, as well as the contribution of first, second and third kernels in spikelets to grain yield and grain protein content, is seldom quantified. The grain yield of main stems and tillers, and the mass of kernels in the spikelet by floret position, were determined in a long-term fertilization and irrigation experiment at the University of Pretoria. A randomized complete block design in a split-plot arrangement with three replicates was used. Main plots consisted of two different soil fertility levels and sub-plots were assigned to four cultivars. Mean grain yield of main stem (MS), first tiller (T_1) and second tiller (T_2) for the cultivar Kariega was 1.26 g, 0.98 g and 0.53 g respectively; 1.29 g, 0.78 g and 0.40 g for Carina; 1.63 g, 0.69 g and 0.09 g for Inia and 1.71 g, 1.10 g and 0.51 g for SST 86. Within a cultivar, the respective ears (MS, T_1 and T_2) did not differ in mean grain protein content, but significant differences were observed among the cultivars with Kariega averaging 16.2% compared to SST 86 and Inia with 14.5%. Main stems contributed on average 68.6%, first tillers 24.8% and third tillers 4.4% of the mean yield per unit area. Main stems produced on average 44.1 grains, first tillers 28.9 grains and the second tillers 15.3 grains. Main stem kernels were 15% larger than kernels from later-formed tillers. Main stems constituted 51.7% of the total ear number per unit area, first tillers 30.3% and the second tillers 14.4%. Mean kernel mass differed with position in the spikelet. First kernels were on the average 9.3% larger than second kernels, and 26.5% larger than third kernels. Main stems and later-formed tillers did not differ in grain protein content. Under the experimental conditions grain yield was largely contributed to by main stems and first tillers, and especially first and second kernels in the spikelet.

Key words: Grain yield, kernel position, main stem, protein content, tiller.

Publications and conference contributions based on this chapter:

Metho, L.A. and Hammes, P.S., 1997. Contribution of main stem, tillers and kernel position to grain yield and protein content of wheat. ***As a Poster of the First All Africa Crop Science Congress, Pretoria, South Africa.***

Metho, L.A., Hammes, P.S. and Beyers, E.A., 1998. The effect of soil fertility on the contribution of main stem, tillers and kernel position to grain yield and grain protein content of wheat. ***S. Afr. J. Plant Soil, 15, 53-60.***

Metho, L.A., Hammes, P.S. and Beyers, E.A., 1998. The effect of soil fertility on the contribution of main stem, tillers and kernel position to grain yield and protein content of wheat. Presented as a ***Poster*** **during the** ***26th SASCP Congress (January 18-22, 1999) in Stellenbosch, Cape Town, South Africa.***

3.2 INTRODUCTION

Knowledge of the relationship of yield in wheat (*Triticum aestivum* L.) with its components (ears per unit area, kernels per ear and kernel mass) have been of great assistance to plant breeders in making selections, although it is now recognised that selections for components of yield may not necessarily result in yield increases. Many researchers have reported on growth analysis as better selection criteria (Stoskopf, Tanner & Reinbergs, 1963; Voldeng & Simpson, 1967; Donald, 1968; Walton, 1971). Other workers have found associations between morphological characters above the flag leaf and yield of wheat (Watson, 1952; Thorne, 1966; Donald, 1968; Rawson & Hofstra, 1969).

Individual wheat shoots differ in grain yield as well as in protein content and hence, in quality (McNeal & Davis, 1954). This is true even of primary shoots of a single genotype grown in a homogeneous plot (Ledent & Moss, 1979). These differences may be accompanied by variation in flag leaf or peduncle morphological development (Ledent, 1974), and may suggest interrelationships between the phenological and morphological development pattern rather than a single trait approach to yield and quality improvement.

Wheat apex development is central to grain yield as both grain number and kernel mass are components of the ear. Wheat cultivars normally produce kernels varying greatly in size as a result of kernel position on the spike (Briggs, 1991). Kernels from the central spikelets of the rachis are larger than those of the basal or distal spikelets (Kirby & Appleyard, 1981; Whingwiri & Stern, 1982).

Within a spikelet, kernels on the basal florets are larger than those of the distal florets and may be controlled by the time of terminal spikelet formation relative to time of floret initiation (Whingwiri & Stern, 1982). Stockman, Fischer & Brittain (1983) found that there are large differences in the strength and size of sinks among spikelets on the same rachis and among florets in the same spikelet, depending on the sink's position. Hay & Walker (1989) showed that central spikelets have advantages in gaining photoassimilates, while spikelets on the distal region of a rachis are the weaker sinks.

McNeal & Davis (1954) found that the earliest formed and matured kernels contained the highest protein content, suggesting a first come-first serve situation regarding translocation of nitrogen to kernels. McNeal, Berg, Brown & Watson (1966) reported a significant negative relationship between grain protein content and harvest index, suggesting that as grain yield makes up a greater part of top growth, grain protein percentages will be correspondingly lower.

Wheat producers often harvest late due to late-maturing tillers, as certain wheat cultivars are known for differential ear development, depending on prevailing environmental conditions. In South Africa it is reported that about 0.5 million tons of wheat received at the silos every year is affected by late-maturing tillers (Wheat Board, 1990; 1994).

The effect of late-maturing ears on grain yield and quality has not been quantified, but is reportedly affecting yield and quality in major wheat growing areas of South Africa. The phenomenon of late tillering in small grain cereals have been reported by others (Aspinall, 1961; Kivisaari & Elonen, 1974).

To explore the relationship between wheat yield and quality the objectives of this study were: (i) to quantify the relative contribution of main stems and tillers, as well as the contribution of first, second and third kernels in the spikelets to yield and protein content, and (ii) to test the hypothesis that tillers affect the quality of grain to a greater degree than their contribution to grain yield. Few studies have been specifically focused on individual kernel mass and quality by relative floret positions in the spikelet, and this may contribute towards strategies in selection for yield and improvement of grain protein content.

3.3 MATERIALS AND METHODS

The experimental details, cultural practices, weather (monthly rainfall, evaporation and mean minimum and maximum temperatures) and statistical procedure are presented in Chapter 2. Because of the repeated measurements on the same experimental unit, a within and between-subject factors ANOVA-procedure was performed to analyse the data using the HELMERT option (SAS User's Guide Stat., 1989).

Main plots consisted of two different soil fertility levels and the sub-plots were assigned to four wheat cultivars. This report only deals with two fertility treatments (NPK and NPKM) representing two well-balanced soil nutrient situations producing strong healthy plants with good yields. Due to the tedious nature of the dissections only three replications were included. At maturity two sets of five plants were randomly sampled and separated into main stems and tiller components.

Ears from the main stems and the tillers were threshed separately, dried at 60^0C for 48hrs, and weighed to obtain grain yield. From the second set of five plants kernels were recovered from any five of the central spikelets (7, 9, 11, 13, 15 and 17 or 6, 8, 10, 12, 14 and 16) and grouped separately into first, second and third kernels. Grain protein content, on a 12% moisture basis, was determined by the Wheat Board on ground samples using a near infrared analyser (NIR)/Dumas Method (AACC, 1989).

3.4 RESULTS AND DISCUSSION

This chapter reports on the main effect of genotype and soil fertility on grain yield per ear, number of fertile ears per unit area, grain number per ear, grain protein content and mean kernel mass at specific floret positions on the ear. Grain yield per unit area, yield components, grain nitrogen content and some interactions between cultivars and soil fertility were reported and discussed in Chapter 2.

Fertile ear numbers

Based on the initial plant population, and tiller ratio of the samples, the number of main stems, first tillers and second tillers were calculated. The cultivars differed in number of ears due to differences in plant populations and tillering potential which resulted in differences in number of fertile ears per unit area (Table 3.1).

The cultivar Inia had the highest plant population and thus number of main stems, while SST 86 had the lowest. First tiller occurrence varied, with Inia having the lowest number, while Carina had the largest number of first tillers.

The four wheat cultivars did not differ in number of second tillers produced, although SST 86 had the highest and Inia the lowest. On the average main stems accounted for 51.7% of the total fertile ear number per unit area, first tillers 30.3% and the second tillers 14.4% and lower order tillers 3.6%. Increasing soil fertility from the NPK treatment to the NPKM treatment significantly increased main stems by 15.3%, first tillers by 13.8% and number of second tillers by 54.5%. In general fertile ear number per unit area increased with increasing soil fertility. Morishima, Oka & Chang (1967) and Hsu & Walton (1971) classified wheat varieties as "ear number" or "ear length" types to emphasize the relative importance of ear number as a component of yield. Other researchers Darwinkel, 1978; Nerson, 1980; Gales, 1983; Bulman & Hunt, 1988) have reported genotypic differences in ability of wheat cultivars to produce fertile tillers.

A positive correlation between spike number and grain yield have been reported by Nass (1973). In our study we obtained a positive and significant correlation between fertile spike number and estimated grain yield (Data not shown)

TABLE 3.1 Effect of wheat cultivars and soil fertility on fertile ear number, main stems, first tillers and second tillers per m^2

Treatment		Fertile number of ears per m ^{2}	Main stems (MS) per m ^{2}	First tillers (T_1) per m ^{2}	Second tillers (T_2) per m ^{2}
CULTIVAR	**SST 86**	442(100)	241(57.0)	129(30.5)	107(25.3)
	Inia	532(100)	378(70.9)	100(18.7)	45 (8.4)
	Kariega	568(100)	253(44.6)	216(38.0)	68 (9.8)
	Carina	674(100)	263(39.0)	220(32.7)	100(14.8)
	LSD_T				
	$P_{\leq 0.05}$	120	49.9	55.2	121
FERTILITY	**NPKM**	575(100)	304(115)	177(114)	96(155)
	NPK	523(100)	264(100)	155(100)	62(100)
	LSD_T				
	$P_{\leq 0.05}$	98	37.2	50.9	93.2
MEAN		549	284	166	79
CV%		15.4	11.4	22.5	101

Figures in ( ) refer to MS, T_1, T_2 as percentage of fertile ear number per m^2 averaged over the NPKM and NPK fertilization treatments.

Grain yield of individual ears

Grain yield of main stems, first tillers and second tillers are shown in Table 3.2. Grain yield of the main stem differed between cultivars, with SST 86 producing the highest yield of 1.71 g and Kariega the lowest (1.26 g). First tiller grain yield did not differ significantly between cultivars and ranged from 0.69 g for Inia to 1.10 g for SST 86. The yield of second tillers was relatively small but differed significantly with that of Kariega being 0.53 g while Inia produced 0.09 g. Yield per square metre was calculated from the number of ears (Table 3.1) and the grain yield of main stems, first tillers and second tillers (Table 3.2). Main stems contributed on average 68.6%, first tillers 24.8% and second tillers 4.4% and the remaining tillers 2.2% of the yield per unit area (Table 3.2).

The estimated grain yield of the cultivars did not differ significantly. Due to the small number of samples (5 plants per treatment) the estimated yield (Table 3.2) differs somewhat from the actual grain yield (Metho, Hammes, De Beer & Groeneveld, 1997). When estimated yields were compared, Inia had the highest and Carina the lowest, while with actual yield Carina produced the highest and SST 86 the lowest. The data show that the main stem (MS) yield was higher and more stable compared to the yield of tillers which varied greatly between the cultivars. Similar results have been reported by Power & Alessi (1978) for spring wheat.

Bulman & Smith (1993) using spring barley (*Hordeum vulgare* L.) reported on the stable nature of main stem ear yield components, and on the relatively small contribution of tillers to grain yield. Gan & Stobbe (1995) reported that main stem grain yield was relatively uniform but tiller yield was highly variable in spring wheat.

Grain yield per ear was highly correlated (r^2 = 0.85) to grain yield per unit area. Nass (1973) using stepwise multiple regression analysis concluded that yield per ear and number of ears per plant, and ears per unit area, made the greatest contribution to grain yield. Briggs (1991) reported that while the productivity of wheat cultivars is determined by both the kernel mass and number of grains, approximately 50% of a plant's productivity in total grains and kernel biomass was produced by the first spike (MS), and 80-90% by the first two spikes (MS and T_1). Our data confirm that grain yield of wheat is largely contributed by main stems and first tillers.

In general increasing soil fertility from the NPK treatment to the NPKM treatment tended to increase grain yield of main stems and that of first tillers, but significantly decreased yield of the second tillers (Table 3.2).

TABLE 3.2 Effects of wheat cultivar and soil fertility on grain yield of main stem, first tiller, second tiller and grain yield per m^2

Treatment		GRAIN YIELD			Estimated [1] grain yield per m^2	Actual [2] grain yield per m^2
		Main stem (MS) (g)	First tiller (T_1) (g)	Second tiller (T_2) (g)	(g)	(g)
CULTIVAR	SST 86	1.71	1.10	0.51	589	390
	Inia	1.63	0.69	0.09	715	448
	Kariega	1.26	0.98	0.53	564	445
	Carina	1.29	0.78	0.40	541	634
	LSD_T $P \leq 0.05$	0.34	0.52	0.23	195	103
FERTILITY	NPKM	1.59	0.99	0.35	684	493
	NPK	1.35	0.78	0.42	521	465
	LSD_T $P \leq 0.05$	0.39	0.31	0.07	172	139
MEAN		1.47	0.96	0.44	602	479
CV%		17.1	37.6	36.4	20.9	20.0

1. Number of MS, T_1 and T_2 per m^2 x mean grain yield per ear of MS, T_1 and T_2.
2. Metho et al., 1997.

Grain number per ear

Grain number per ear is the product of number of fertile spikelets per ear and grains per spikelet, while grains per unit area is a function of number of grains per ear and ears per unit area. Grain number varied with cultivar, with SST 86 having the largest number of grains per ear, averaging 32.3 grains, and Inia the lowest with 24.5 grains (Table 3.3).

Although not statistically significant, SST 86 had the highest number of grains per ear in the main stems, first tillers and second tillers, while Inia had the lowest numbers. Main stems produced on average 44.1 grains, first tillers 28.9 grains and the second tillers 15.3 grains. On a single plant basis, mean whole plant grain number was 73.4 grains for Inia, 89.5 grains for both Kariega and Carina, and 96.9 grains for SST 86.

Increasing soil fertility from the NPK treatment to the NPKM treatment did not significantly affect grain number per ear or per main stem, but significantly increased grain number of the first tillers by 24%. The number of grains of the second tillers (T_2) was not significantly affected, although increased by 13.3% (see Table 9.A6). In field experiments, several authors (Puckridge & Donald, 1967; Willey & Holliday, 1971; Fischer, Aquilar, Mauver & Rivas, 1976) have reported that increase in grain yield was positively correlated with an increase in grain number.

Results indicate that grain yield per ear was strongly associated with grain number per ear. The high yield of main stems compared to that of tillers led to a wheat with one culm being identified as crop ideotype by Donald (1968). The advantages of tillers for grain production and for compensation purposes remain debatable due to differences in the grain yield of main stems and tillers. Ledent & Moss (1979) reported a close association between kernel number and shoot or ear yield, while Nass (1973) reported that kernels per ear and kernel weight were associated with yield per ear. Later-formed shoots produced ears that contained fewer grains due to reduced number of fertile spikelets (Darwinkel, 1978). Bulman & Smith (1993) reported that poor grain yield of tillers resulted from the formation of fewer and smaller grains.

TABLE 3.3 Effect of wheat cultivar and soil fertility on mean grain number of main stems, first tillers, second tillers and of whole plant

Treatment		GRAIN NUMBER				
		Main stem (MS)	First tiller (T_1)	Second tiller (T_2)	Mean grain[1] number per ear $\frac{(\Sigma MS + T_1 + T_2)}{3}$	Whole plant grain number (WP)
CULTIVAR	**SST 86**	46.8	31.7	18.5	32.3	96.9
	Inia	40.9	23.0	9.5	24.5	73.4
	Kariega	44.9	31.7	16.9	29.9	89.5
	Carina	43.9	29.3	16.2	29.8	89.5
	LSD_T $P_{\leq 0.05}$	8.44	10.2	9.2	6.1	18.3
FERTILITY	**NPKM**	44.9	32.0	16.2	31.2	93.1
	NPK	43.3	25.8	14.3	27.1	81.6
	LSD_T $P_{\leq 0.05}$	7.1	5.7	5.5	5.6	16.9
MEAN		44.1	28.9	15.3	29.2	87.4
CV%		12.9	22.4	38.3	14.4	14.3

1. Averaged over the NPKM and NPK fertilization treatments.

Kernel mass

The effects of cultivar and soil fertility on kernel mass are shown in Table 3.4. The cultivars differed in mean kernel size of the main stems with Inia having the largest kernels averaging 39.8 mg, while Carina had the smallest kernels at 29.3 mg. Kernels on main stems were on average 15% larger than kernels from the later-formed tillers (T_1 and T_2), probably due to limiting photoassimilate supply in the case of tillers.

Kernels from the first tillers differed with Inia kernels averaging 34.1 mg and Carina 26.8 mg. Kernels from the second tillers did not differ significantly, although they ranged in size from 22.9 mg to 30.6 mg. Hsu & Walton (1971), from a factor analysis for both greenhouse and field trials, reported that 20.9% of the total variation in yield was attributed to 1000 kernel mass. Darwinkel (1978) reported that at higher plant densities there was no relationship between shoot age and grain weight, but when kernels from shoots or ears which emerged first were compared to those that emerged later, it was found that the former had larger and heavier kernels than those from later-formed ears. Kernel mass depends on the availability of plant assimilates during the stage of grain-filling, and this is closely related to the leaf area duration after anthesis (Spiertz, Ten Hag & Kupers, 1971; Thorne, 1974; Annandale, Hammes & Nel, 1987). Puckridge & Donald (1967) and Willey & Holliday (1971) found that very high numbers of grains can only be achieved in dense crops, in which radiant energy for grain-filling will be limited and grain weight will decrease due to less reserve carbohydrate in ear-bearing shoots after anthesis. Briggs (1991) concluded that genotypic variation in kernel mass (or seed size) within wheat cultivars is common and will depend on the levels of environmental stress in a particular growing season as well as on the specific plasticity of individual cultivars. Although not statistically significant, kernel mass tended to increase with increase in soil fertility (Table 3.4). Many workers (Terman, Ramig, Dreier & Olson, 1969; Ledent & Moss, 1979; Bulman & Smith, 1993) have reported that response of kernel mass or grain weight to climatic conditions, nitrogen treatments or soil fertility generally vary. Application of N-fertilizer treatments from 0 to 200 kg N per ha did not affect 1000-grain weight in an experiment conducted by Bulman & Smith (1993).

Wheat yield is generally attributed to three primary components namely number of ears per unit area, number of grains per ear and mean kernel mass. Variations in yield per shoot result from differences in kernel number per ear and kernel mass. Correlations between yield per plant and its primary components (ears per plant, grain number per ear and mean kernel mass) both in green house and field conditions have often been reported (Hsu & Walton, 1970; 1971; Bulman & Hunt, 1988). While acknowledging the contribution of other researchers, considerable effort is still needed to enhance our understanding of how genotypes and soil fertility interact in relation to the role of ears as sinks, and kernel size distribution between individual ears and within the different spikelets.

The results show that wheat cultivars differ in grain yield potential of individual ears. Main stem yield was relatively high and stable compared to the yield of later-formed tillers which varied greatly between the cultivars. Similar results have been reported by among others Power & Alessi (1978). Gan & Stobbe (1995), working with spring wheats, reported that main stem grain yields were relatively uniform but tiller grain yields were highly variable. Tillers contributed poorly due to fewer grains and smaller kernel mass. The results show that kernel size depends on position of ear, whether main stem or from later-formed tillers. Our data confirms those reported by Levi & Anderson (1950) and Briggs (1991) who found differences in kernel mass in different positions in the spike and spikelet. The data indicate that, under the experimental conditions, grain yield of wheat is largely contributed by main stems and first tillers, and especially first and second kernels in the spikelet.

Grain protein content per ear

The protein content of the ears varied as shown in Table 3.5. Main stems differed with Kariega having 16.2% protein and SST 86 having 14.5%. The first tillers did not differ in grain protein content and varied from 14.7% to 15.6%. In the case of second tillers the cultivars differed in grain protein content with Kariega having 16.2% protein, while Inia contained 14.5%.

Levi & Anderson (1950) and McNeal & Davis (1954) reported small, and not significant differences in protein percentage between the main stems, tillers and composites. The relatively high protein values (14.2-16.2%) obtained in my study is typical for very small samples of grain, according to Randall (Personal communication, 1997). The treatments NPK and NPKM did not differ in grain protein content, except in second tillers where grain protein content in the NPKM treatment significantly increased. Large differences in grain protein was observed in other fertility treatments of this experiment, indicating grain protein increased with improved soil fertility status (Appendix Table 9.A7.). Schlehuber & Tucker (1959), Johnson, Schmidt, Mattern & Haunold (1963), Laubscher (1981) and Fischer (1989) have reported improved grain protein content and higher grain yield of wheat with improved soil fertility. The same authors reported that the major factors affecting grain protein are climate, soil fertility and genotype. The benefits of applying nitrogen fertilizer to increase both yield and grain protein levels in wheat have been reported by many research workers (McNeal & Davis, 1954; Finney, Meyer, Smith & Fryer, 1957; Seth, Herbert & Middleton, 1960; Alkier, Raczs & Soper, 1972; Strong, 1982; Randall, Freney, Smith, Moss, Wrigley & Galbally, 1990). Inverse relationships between protein content of wheat grains and yield level have also been reported (Malloch & Newton, 1934; Terman, Ramig, Dreier & Olson, 1969).

Kernel mass and grain protein content in floret positions 1, 2 and 3 in the spikelet

Differences between cultivars in kernel mass and grain protein content for the different kernel positions in the spikelet are shown in Tables 3.6 and 3.7. In floret position 1 the cultivar SST 86 had the largest kernel mass averaging 42.4 mg, while Kariega kernels were the smallest at 37.8 mg. Kernels in floret position 2 differed with Inia having the largest kernels at 39.5 mg, and Kariega the smallest averaging 34.0 mg. In floret position 3, Inia produced the largest kernels averaging 35.9 mg, while Carina had the smallest averaging 21.5 mg. Floret position affected kernel size the least in cultivar Inia, where kernels from floret 3 were 14.3% smaller than those from floret 1. The cultivar Carina showed the largest variation in kernel size, as third kernels were 46% smaller than first kernels (Table 3.6). The 1st and 2nd kernels did not differ in mass, but kernels in 3rd position in the spikelet were significantly smaller compared to the 1st and 2nd kernels in all cultivars. Kernels from central spike positions were significantly larger than kernels from the basal and distal end of the spike (data not shown). These results are based on the data collected on the well-formed central spikelets, as distal or basal spikelets varied greatly in number of grains produced and in kernel size.

TABLE 3.4 Effect of wheat cultivars and soil fertility, on mean kernel mass of main stem, first tiller and second tiller

Treatment		MEAN KERNEL MASS		
		Main stem (MS) mg	First tiller (T_1) mg	Second tiller (T_2) mg
CULTIVAR	**SST 86**	36.4 (100)	30.3 (83.2	30.6 (84.1)
	Inia	39.8 (100)	34.1 (85.7)	30.4 (76.1)
	Kariega	31.1 (100)	29.9 (91.5)	28.9 (92.9)
	Carina	29.3 (100)	26.8 (91.5)	22.9 (78.2)
	LSD_T			
	$P_{\leq 0.05}$	5.8	6.9	11.4
FERTILITY	**NPKM**	35.7 (110)	30.3 (103)	29.5 (108)
	NPK	32.6 (100)	28.6 (100)	28.2 (100)
	LSD_T			
	$P_{\leq 0.05}$	7.6	3.6	7.9
MEAN		34.2	29.5	28.8
CV%		12.9	14.1	23.6

Figures in ( ) are expressed as percentages relative to kernel mass of MS.

TABLE 3.5 Effect of wheat cultivars and soil fertility on mean grain protein content of main stem, first tiller and second tiller

Treatment		MEAN PROTEIN CONTENT (%)		
		Main stem (MS)	First tiller (T_1)	Second tiller (T_2)
CULTIVAR	**SST 86**	14.5	15.3	15.8
	Inia	14.5	14.7	14.5
	Kariega	16.2	15.6	16.2
	Carina	15.7	14.9	14.9
	LSD_T			
	$P_{\leq 0.05}$	1.82	1.58	0.98
FERTILITY	**NPKM**	15.2	15.6	16.2
	NPK	15.2	14.7	14.5
	LSD_T			
	$P_{\leq 0.05}$	1.05	1.22	0.15
MEAN		15.2	15.1	15.3
CV%		7.6	6.9	3.9

TABLE 3.6 Mean mass of kernels in floret positions 1, 2 and 3 in the spikelet of four South African wheat cultivars

Treatment		MEAN KERNEL MASS		
		Floret position 1 (mg)	Floret position 2 (mg)	Floret position 3 (mg)
CULTIVAR	SST 86	42.4 (100)	38.7 (91.3)	32.7 (77.1)
	Inia	41.9 (100)	39.5 (94.3)	35.9 (87.7)
	Kariega	37.8 (100)	34.0 (89.9)	28.3 (74.9)
	Carina	39.8 (100)	35.6 (89.4)	21.5 (54.6)
	LSD_T $P_{\leq 0.05}$	3.93	4.26	5.64
FERTILITY	NPKM	41.7 (106)	37.6 (104)	27.3 (85.6)
	NPK	39.3 (100)	36.3 (100)	31.9 (100)
	LSD_T $P_{\leq 0.05}$	4.02	3.74	3.54
MEAN		40.5	36.9	29.6
CV%		6.9	7.8	11.8

TABLE 3.7 Mean protein content of grains in floret positions 1, 2 and 3 in the spikelet of four South African wheat cultivars

Treatment		MEAN PROTEIN CONTENT (%)		
		Grains in floret position 1	Grains in floret position 2	Grains in floret position 3
CULTIVAR	SST 86	15.4	15.4	14.2
	Inia	14.8	14.8	14.1
	Kariega	16.4	16.0	14.3
	Carina	15.8	15.5	14.7
	LSD_T $P_{\leq 0.05}$	1.01	1.33	1.19
FERTILITY	NPKM	15.9	15.9	14.5
	NPK	15.2	41.9	14.1
	LSD_T $P_{\leq 0.05}$	0.74	1.44	0.64
MEAN		15.6	15.4	14.3
CV%		4.2	5.9	5.3

Wheat normally produces kernels varying greatly in size as a result of kernel position on the spike (Briggs, 1991). Gan & Stobbe (1995) reported that kernels from the central spikelets of the rachis are larger than those of the basal or distal spikelets, and within a spikelet, kernels on the basal florets are larger than those of the distal florets. Briggs (1991) concluded that smaller kernels result partly from floret position effects and partly from kernel mass reduction for later-formed tillers. Grain protein content for kernels from floret position 1 varied between cultivars with Kariega having 16.4% protein, and Inia 14.8% (Table 3.7).

Grain protein content did not differ between cultivars in floret positions 2 and 3. In floret position 2 grain protein ranged from 14.8% to 16.0%, while for floret position 3 protein content varied from 14.1% to 14.7%. When grain protein content of kernels in floret position 3 was compared with those in floret position 1, Inia showed the least variation in protein content while Kariega varied most (Tabel 3.7; Appendix Table 9.A8). The data confirms those reported by Levi & Anderson (1950) and McNeal & Davis (1954) who found that earliest formed and matured kernels contained the highest protein content, suggesting a "first come-first serve" situation as regards translocation of nitrogen from plant tissues to kernels. More recently Jenner, Ugalde & Aspinall (1991) reported that under adequate growing conditions, both rate and duration of starch deposition during grain filling are determined mainly by factors that operate within or close to the grain itself. The rate and duration of protein deposition are determined by factors of supply external to the grain. The same authors suggested that grain yield and grain protein percentage should be selected as independent traits in cultivar improvements.

Increasing soil fertility from the NPK treatment to the NPKM treatment resulted in slight increases in grain protein content of kernels. Elevated grain protein have resulted from crosses of cultivated wheat and wheat-related species, in addition to application of N-fertilizer and breeding for cultivars efficient in N uptake and translocation (Fischer, 1989).

3.5 CONCLUSIONS

The effect of soil fertility on the relative contribution of main stems and fertile tillers were quantified. In general main stems (MS) contributed 69%, first tillers (T_1) 25%, second tillers (T_2) 4% and the remaining tillers 2% of the mean yield per unit area, depending on cultivar and growing situation. On the average, main stems accounted for 52% of the total fertile ear number per unit area, first tillers 30% and the second tillers 14%, and lower order tillers 4%. Relative kernel mass and protein content generally declined in the spikelet from the 1st to the 3rd floret position.

Tiller contribution to yield was low compared to that of main stems. The protein content of main stems and tillers did not differ, thus disproving the initial hypothesis that tillers may affect grain quality.

The relative contribution of main stems and tillers, as well as the relative contribution of first, second and third kernels in spikelets to grain yield and protein content, are seldom quantified. The data presented are rarely available, because the process is often tedious and time consuming, but valuable to crop modellers and users, and may be utilized in agronomic management strategies and crop modelling in different environments for optimum yield and quality.

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CHAPTER 4

THE HARVEST INDEX OF INDIVIDUAL EARS OF FOUR SOUTH AFRICAN WHEAT (*TRITICUM AESTIVUM* L.) CULTIVARS

4.1 ABSTRACT

Increasing the harvest index is a major route to higher yields in regions where a crop has had a lengthy period of selection and adaptation. No information could be found on differences in the harvest indices of the main stems and tillers of South African wheat cultivars. Consequently, this was determined for four wheat cultivars grown in a long-term fertilization and irrigation experiment at the University of Pretoria. A randomized complete block design in a split-plot arrangement, with three replicates, was used. The four cultivars did not differ in main stem (MS) harvest indices with a mean of 0.44. The harvest index of first tillers (T_1) differed significantly with SST 86 having the highest (0.48) and Carina the lowest (0.29), with that of Kariega and Inia intermediate between SST 86 and Carina. The low harvest indices of second tillers (T_2) indicate less effective utilization of resources by the tillers. The data indicates that individual wheat ears differ in the partitioning of assimilates to the grain and this may help in identifying genotypes more efficient in assimilate utilization for improved yield.

Key words: Biological yield, harvest index, main stem, tiller, *Triticum aestivum* L.

Publication based on this study:

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4.2 INTRODUCTION

Migration Coefficient or Harvest Index is the proportion of dry matter of the entire ripe plant, excluding roots, that is accumulated in relation to the grain (Engledow & Wadham, 1923; Donald, 1962). In cereals, economic yield is the product of biological yield and harvest index

(Donald, 1962; Siddique & Sedgley, 1985). Donald & Hamblin (1976) argued that yield improvements could be achieved if a high harvest index was selected for in a competitive environment. Siddique, Kirby & Perry (1989) concluded from their study of ear:stem ratio's in old and modern wheat varieties grown in south-western Australia that improvement in grain yield resulted from reduced competition between stem and ear for dry matter, associated with a long-term trend towards a shorter life cycle and fewer stems. Fisher (1984), Amollo-Ocholla, Sedgley & Seaton (1986) and Amollo-Ocholla (1987) reported for cultivars widely grown in Western Australia an increasing yield trend with date of release. Increased yields were associated with increased harvest indices, reduced tillering capacity and earlier floret development. Other studies of historical cultivars generally show that increases in the potential grain yield were linked to increases in the harvest index (Blum, 1989; Austin, Bingham, Blackwell, Evans, Ford, Morgan & Taylor, 1980).

Fischer & Kertzer (1976) concluded that under optimal conditions of moisture and fertilizer application the harvest index offered promise as an early generation predictor of performance. On the other hand, Whan, Rathjen & Knight (1981) found that selection for improvement of grain yield using harvest index was no more effective than selection for yield directly, when considered across years. Rasmusson (1987) suggested that early generation selection for harvest index and for proven characters, followed in later generations by selection for yield stability across environments may, result in improved grain yield.

The main objective of this study was to extend the concept of harvest index to the individual shoots of a wheat plant using four South African wheat cultivars. Understanding harvest index differences among tillers can contribute towards improved breeding and selection, better crop modelling and improved yield prediction strategies.

4.3 MATERIALS AND METHODS

A long term-term fertilization and irrigation trial at the Hatfield Experimental Farm of the University of Pretoria was used. The experimental details, cultural practices, weather and statistical procedures are described in Chapter 2 and in Metho, Hammes, De Beer & Groeneveld (1997) and Metho, Hammes & Beyers (1998). In this study two soil fertility treatments (NPK and NPKM), representing well-balanced soil fertility situations, are considered (data not shown). Four cultivars Inia, Carina, Kariega and SST 86, treated as the split-plots were randomly sampled and separated into main stems (MS), first tillers (T_1), second tillers (T_2), and third tillers (T_3). Ears from the respective wheat shoots (MS, T_1, T_2 and T_3) were threshed separately, dried at 60 ^{0}C for 48 hrs, and weighed. Similarly, leaf and straw dry mass were determined. Harvest index was calculated as the ratio of grain yield to aboveground dry matter at maturity.

4.4 RESULTS AND DISCUSSION

The main effects of soil fertility and cultivar on harvest index of individual fertile wheat ears are presented in Table 4.1. Because of the erratic occurrence of higher order tillers (e.g. T_3, T_4) only main stems, first and second order tillers are discussed. Grain yield of main stems (MS), first tillers (T_1), second tillers (T_2), as well as relative mass of kernels and grain protein content in floret positions 1, 2, and 3 were discussed Chapter 3 and by Metho, Hammes & Beyers (1998).

Harvest index of individual wheat ears

The cultivars did not differ in mean harvest index and main stem harvest indices (Table 4.1). The harvest index of the cultivar SST 86 averaged 0.42 showing a high efficiency in carbon distribution to the ear. For the cultivars Inia, Kariega, and Carina the harvest indices were in the range of 0.34 to 0.36. This differs somewhat from the bulk harvest index values obtained on a plot basis as reported in Table 2.4.

Grain yield depends on effective translocation of current photosynthates to the grain, and is a more constant characteristic than biological yield for plants or varieties (Engledow & Wadham, 1923). Vogel, Allen & Patterson (1963) and Syme (1970) reported a significant correlation between grain yield and harvest index. The concept of harvest index when applied to the individual shoots of a plant may be useful in identifying characters that might increase yield (Takeda, Frey & Bailey, 1980). Islam & Sedgley (1981) for spring wheat, and Siddique & Sedgley (1985) for chickpea, reported that control of tillering or branching may maximize yield per ear.

Harvest indices of the first tillers differed significantly with SST 86 having the highest harvest index of 0.48 and Carina the lowest (0.29), while that of Kariega was intermediate (0.36). The second tillers did not differ significantly in harvest index, with indices between 0.22 and 0.33. On an individual shoot basis Inia exhibited the largest variation in shoot harvest index while SST 86 varied the least. For Carina first and second tillers did not differ (Table 4.1). The interaction between cultivar and soil fertility was not significant for harvest index.

TABLE 4.1 Effects of cultivar and soil fertility on mean harvest index, harvest index of main stem, first tiller and second tiller of four South African wheat cultivars

Treatment	Mean harvest index	HARVEST INDEX (H1)		
	$\frac{(\Sigma MS + T_1 + T_2)}{3}$	Main stem (MS)	First tiller (T_1)	Second tiller (T_2)
CULTIVAR				
SST 86	0.42	0.46	0.48	0.33
Inia	0.36	0.46	0.40	0.22
Kariega	0.35	0.41	0.36	0.27
Carina	0.34	0.43	0.29	0.29
LSD_T $P_{\leq 0.05}$	0.12	0.16	0.10	0.21
CV%	19.9	14.4	16.3	43.5

4.5 CONCLUSIONS

The data indicate that wheat cultivars differ in individual ear harvest indices and in the degree of partitioning of assimilates to the grain, and hence in effective utilization of resources. Understanding differences among tillers may help in identifying genotypes with improved yield potential in early stages of wheat breeding and selection.

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CHAPTER 5

EFFECTS OF CULTIVAR AND SOIL FERTILITY ON GRAIN PROTEIN YIELD, GRAIN PROTEIN CONTENT, FLOUR YIELD AND BREAD-MAKING QUALITY OF WHEAT

5.1 ABSTRACT

Grain protein content affects bread-making quality characteristics of wheat (*Triticum aestivum* L.). In this study grain protein yield, grain protein content, flour yield and loaf volume were quantified for four wheat cultivars (Inia, Carina, Kariega and SST 86) grown at six different soil fertility regimes in a long-term fertilization and irrigation experiment at the University of Pretoria. The experimental design was a randomized complete block replicated four times, with fertility as the main-plots and cultivars as the sub-plot treatments. Grain protein yield, flour yield, loaf volume and mixograph dough peak mixing time varied between cultivars and soil fertility situations. Grain protein content differed between cultivars but mixograph water absorption and dough characteristics did not differ. The highest grain protein yield was 873 kg ha^{-1} for Carina, and the lowest 527 kg ha^{-1} for SST 86. Grain protein content averaged 13.1% for Carina and 12.2% for Kariega. Bread-making performance showed that in a well-balanced soil fertility situation, Kariega produced 1025 cm^3 of loaf volume while Inia averaged 950 cm^3. Grain protein yield increased with increasing soil fertility but grain protein content, flour yield, loaf volume, water absorption and mixograph peak mixing time did not vary in a consistent pattern with changing soil fertility. The interaction between cultivar and soil fertility was significant for grain protein yield, grain protein content, flour yield, loaf volume and water absorption, but not for peak dough mixing time. The results indicate cultivar differences in bread-making quality characteristics, and that soil fertility status affects grain protein yield, grain protein content, flour yield, loaf volume potential, water absorption, but not mixograph peak mixing time and dough characteristics.

Key words: Bread-making quality, flour yield, grain protein, soil fertility, wheat.

Publications and conference contribution based on this study:

Metho, L.A., Taylor, J.R.N., Hammes, P.S. & Randall, P.G., 1999. Effects of cultivar and soil fertility on grain protein yield, grain protein content, flour yield and bread-making quality of wheat. *J. Sci. Food Agric.* 79, 1823-1831.

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5.2 INTRODUCTION

The relationship between wheat (*Triticum aestivum* L.) grain protein content and bread-making quality has been well established (Bushuk, Rodriquez-Bores & Dubetz*,* 1978; Payne Corfield, Holt & Blackman, 1981; Payne, Holt, Jackson & Law, 1984). Wheat grain protein content is important in bread-making because high protein flours generally have a high loaf volume potential, high water absorption and produce loaves with good keeping quality (Finney, Meyer, Smith & Fryer*,* 1957). The grain protein content of wheat is genetically controlled, but may vary widely for a given variety or cultivar according to location, soil fertility, rainfall or temperature (Moss, 1973; Laubscher, 1981). The plant-available soil N affects grain protein which determines bread-making quality. Wheat protein content may also be increased by breeding and selection for N use efficiency (Noaman, Taylor & McGuire, 1987; Fischer, 1989).

Increases in wheat grain protein with application of N fertilizers have been reported (Finney *et al.,* 1957; Dubetz, 1972). Correcting a soil fertility deficiency may result in higher economic returns from better grade for the producer (Hunter & Stanford, 1973; Laubscher, 1981). Grain protein content when studied independently of other plant characteristics acts as an inherent trait (Haunold, Johnson & Schmidt, 1962; Johnson, Schmidt & Mattern, 1968), but studied in conjuction with related characteristics, it seems largely determined by plant growth responses (Fischer, 1989; Cox, Qualset & Rains*,* 1985).

Positive correlations between grain protein content and loaf volume have been reported by many researchers (Finney *et al.,* 1957; Schlehuber & Tucker 1959; Pendleton & Dungan, 1960; Terman, Ramig, Dreier & Olson*,* 1969). Johnson *et al,* (1968), Borghi, Corbellini, Cattaneo, Fornasari & Zucchelli (1986) and Perenzin, Pogna & Borghi (1992) reported wheat progeny with high grain protein content. Increasing grain protein content have been obtained by applying N fertilizer (Bauer, 1970; Dubetz, 1972). Laubscher (1981) also reported increased grain protein content from improved soil nutrient concentrations. Genotype and environment interaction, however, plays a major role in determining protein level (Moss, 1973; Laubscher, 1981).

Attempts have been made to establish a molecular basis for wheat proteins responsible for bread-making quality (Payne *et al.,* 1981; 1984; Anderson, Blechl & Weeks*,* 1995). Randall, Manley, McGill & Taylor (1993) reported a close association between the presence of certain high-molecular-weight (HMW) subunits of glutenin with the bread-making quality of South African bread wheat cultivars.

The HMW-glutenins are highly correlated with specific parameters important for dough functionality (MacRitchie, Kasarda & Kuzmicky*,* 1991; Randall *et al.,* 1993). The total amount of HMW glutenins have been reported to determine the strength characteristics of bread doughs (Blechl & Anderson 1998).

Grain protein content is, however, still one of the most important single factors causing variation in bread-making quality potential of wheat genotypes (Pomeranz, 1973; Laubscher, 1981). It is apparent that soil fertility, and especially soil N, plays a major role in grain protein level (Liang, Heyne & Walter*,* 1966; Lee & Spinalle, 1970; Carr, Jacobsen, Carlson & Nielsen*,* 1992). Improving grain protein content will depend on increasing soil fertility status and/or using cultivars with the ability to produce higher yield and improved grain protein content under nutrient limiting growing situations. This may be important for South Africa, where a higher price is normally paid for class B with grain protein equal to or greater than 12% (Wheat Board 1994,1995).

The objectives of this study were: (i) to quantify the effects of varying soil fertility on grain protein yield, grain protein content, flour yield and bread-making quality of four South African wheat cultivars, and (ii) to test the hypothesis that all these characters are affected by soil fertility and varying soil nutrient situations.

5.3 MATERIALS AND METHODS

General

Four wheat cultivars Inia, Carina, Kariega and SST 86 were grown at Hatfield Farm, University of Pretoria (Lat. 25^0 45'S, Long. 28^0 16'E, elevation 1372 masl), using a long-term fertilization and irrigation experiment started in 1939. The experimental design was a randomized complete block replicated four times, with soil fertility as the main-plot and cultivars as the sub-plot treatments. The cultivars were planted in unrandomized strips on the sub-plots. Main plot size was 8.25 m by 6.30 m and the sub-plot size 1.20 m by 6.30 m. Experimental treatments are given in Table 5.1, and weather data in Table 5.2. Detailed experimental procedures were reported in Chapter 2 and in Metho, Hammes, De Beer & Groeneveld (1997).

Soil analysis data are presented in Table 5.3 for the 0-200 mm soil layer for the selected treatments, and reflect the actual site pH and fertility status representing the effect of differential fertilization over more than 50 years. In general, soil analysis of the individual plots (NPKM, NPK, PK, NP and NK treatments) indicate differences in soil pH, N, P, and K status maintained under long-term fertilization. The site soil details were described by Nel, Barnard, Steynberg, De Beer & Groeneveld (1996).

Protein content analysis

Grain protein (N X 5.7) was measured by a Kjeldahl method (A.A.C.C., 1989 method 46-12) and by Dumas method (A.A.C.C., 1989 method 46-30), and expressed on dry weight and 12% moisture.

Grain protein yield

Grain protein yield (g m^{-2}) was calculated as: grain yield (g m^{-2}) x grain protein content (%) /100.

Flour yield and quality assessment

Wheat samples were conditioned to 12.0% moisture for 20 hours, and milled using the Quadrumat mill (A.A.C.C., 1989 method 54-30). This accounts for the very low atypical percentage flour yields obtained. For the dough tests, the Mixograph method was used (A.A.C.C., 1986 method 46-30). Bread-making tests were by the method of Moss (1980) on breeder's standard 100 g sample loaves.

Data recorded

Plants from a 1 m^2 area were harvested at physiological maturity. Grain yield (g m^{-2}), mean grain weight (g), grain protein yield (g m^{-2}), and grain protein content (%) were determined from the 1 m^2 bulk samples. To cause minimum interference with long-term rotation practices only treatments ‘O’ Control, NPK and NPKM were retained for determination of grain protein yield, grain protein content and flour yield in the case of the late maturing cultivar Carina.

To get an indication of bread-making quality, analysis was performed based on only two of the four wheat cultivars (Inia and Kariega) grown under four fertility treatments (NPK, PK, NP and NK) where NPK plots represent a well-balanced soil fertility situation producing strong healthy plants with good yield, while the other treatments represented N, K and P limiting soil fertility situations.

Table 5.1 Details of experiment conducted on four local wheat cultivars grown under irrigation at Hatfield, Experimental Farm, University of Pretoria

Practices	Long-term fertility experiment
Crop rotation	Wheat grown during the winter period may to October and soybean from November to March, except the year prior to 1995 when the plots were fallowed during summer.
Planting date	15 and 16 May using Planet Junior, planter USA.
Wheat cultivars	Inia – Pureline, semi-dwarf spring type released in 1966 by the Department of Agriculture. Carina – Hybrid, semi-dwarf winter type released in 1989 by Carnia Kariega – Semi-dwarf spring type released in 1993 by the Small Grain Institute (SGI). SST 86 – Dwarf spring type, released in 1987 by Sensako.
Seeding rate (Based on seed size)	Inia – 100 kg ha^{-1} Carina – 70 kg ha^{-1} Kariega – 100 kg ha^{-1} SST 86 – 150 kg ha^{-1}
Nutrient treatments	N – 100 kg N ha^{-1} (KAN 28%) P – 70 kg P ha^{-1} (Single superphosphate, 8.3%) K – 50 kg K ha^{-1} (Potassium chloride 50%) M – 15 tons ha^{-1} (Farmyard manure) Lime – 180 kg ha^{-1} (Agricultural lime, $(Ca(OH)_2 + MgSO_4)$
Diseases & Pests	No major disease was recorded. Loose smut (*Ustilago tritici*) was controlled by removing infected plants. Harvester termites (*Hodotermes sp*) was controlled by Parathion (Folimat, WP) at 1.5 kg ha^{-1}. Birds controlled with netting.
Maturity	Inia and SST 86 reached physiological maturity on 16 October, Kariega on 23 October and Carina by 16 November.

TABLE 5.2 Meteorological data for Hatfield Farm in 1995 and long-term mean rainfall (1974-1995)

Months	Temperature (°C)		Pan evaporation	Rainfall	Long-term rainfall
	Max	Min	(mm/day)	(mm/day)	(mm/month)
January	29.3	16.8	8.2	69.8	126.1
February	30.3	16.6	8.2	103.4	109.0
March	26.6	15.4	6.1	168.8	98.2
April	23.6	11.0	4.9	80.8	39.7
May	20.4	8.3	3.4	7.0	11.6
June	19.2	2.6	3.3	0.0	6.5
July	19.6	4.0	4.2	0.0	3.8
August	22.8	7.4	5.4	5.0	6.6
September	27.0	11.4	7.5	3.5	20.2
October	27.7	14.3	8.0	63.2	71.6
November	27.2	15.3	7.9	213.0	105.2
December	26.5	14.5	7.3	154.7	119.6
Year	25.0	11.5	74.4	868.8	717.6

Table 5.3 Soil analysis (0-200 mm) results for experimental site, 1995

Treatment	pH (H_2O)	Bray 2 P mg kg^{-1}	K mg kg^{-1}
NPKM	5.8	109	120
NPK	5.4	63	66
PK	6.0	43	92
NP	5.1	37	21
NK	5.2	1,8	81
Control "O"	6.1	1,7	22
CV %	3.7	46.5	49.1

Statistical analyses

Data was analysed by analysis of variance using the SAS/STAT programme (SAS Institute Inc. Cary, NC., USA 1989 Copyright). Differences at the $P \leq 0.05$ level of significance are reported. Tests for heterogeneity of variances for all characteristics were done and probabilities calculated according to Steel & Torrie (1980). Direct correlation and stepwise regression analyses were performed to determine the relationship between loaf volume and rain protein yield, grain protein content, flour yield, water absorption, mixograph peak dough mixing time and soil fertility.

5.4 RESULTS

The main effects of genotype and soil fertility on grain protein yield, grain protein content, flour yield and bread-making quality (water absorption, mixograph peak dough mixing time, loaf volume and dough characteristics) are shown in Tables 5.4, 5.5, 5.6 and 5.7 respective-ly. Significant cultivar and soil fertility interactions were observed for grain protein yield, grain protein content, flour yield, loaf volume and water absorption, and are illustrated in Figure 5.1.

The main effects of cultivar and soil fertility on grain yield, yield components and grain nitrogen content and significant interactions are reported in Chapter 2 and in Metho *et al*. (1997).

Effect of cultivar

Grain protein yield

Under conditions of the experiment, grain protein yield differed with Carina producing the highest protein yield (873 kg ha^{-1}) and SST 86, Inia and Kariega producing lower yield in the range 527, 539 to 586 kg protein ha^{-1} (Table 5.4).

Grain protein content

The cultivars differed significantly in grain protein content (Table 5.4; Tables 9.A9 and A.10). The cultivar Carina had the highest grain protein content averaging 13.1% while SST 86, Inia and Kariega had significantly lower grain protein contents in the range 12.2% to 12.6%. Table 5.4 shows that the cultivars differed in high molecular weight sub-units of glutenin but not in Glu-1 score.

Flour yield

Flour yield differed significantly between the cultivars (Table 5.4). The cultivar Kariega had the highest flour yield averaging 53.6% but did not differ significantly from Inia (51.8%), while SST 86 (47.7%) and Carina (48.7%) had lower flour yields and did not differ significantly.

Loaf volume

Loaf volume comparisons were made for only Inia and Kariega (Table 5.6). The cultivars differed in loaf volume, and averaged over all fertility levels Kariega produced on average 981 cm^3 of loaf volume and Inia 910 cm^3 (Table 5.6; Appendix Table 9.A9).

Mixograph water absorption, mixograph peak mixing time and dough characteristics

The two wheat cultivars Inia and Kariega did not differ significantly in mixograph water absorption and peak mixing time (Table 5.6).

TABLE 5.4 Effects of cultivar on grain protein yield, grain protein content, high-molecular weight glutenins, glu-1 score and flour yield of four South African wheat cultivars

Cultivar[1]	Grain protein yield (kg ha^{-1})	Grain protein content (dry basis) (%)	High-molecular[2] weight glutenins (HMW-GS)	Glu-1 score[2]	Flour yield[3] (%)
SST 86	527a[+]	12.6a	(13 + 16) (5 + 10)	3	47.7a
Inia	539a	12.6a	(13 + 16) (5 + 10)	3	51.8b
Kariega	586a	12.2a	(17 + 18) (5 + 10)	3	53.6b
Carina	873b	13.1b	-	-	48.7a
CV %	22.3	6.9			6.2

+ Within columns, means followed by the same lowercase letter had P > 0.05 and hence were not significantly different according to an Duncan's multiple range test.

1 Cultivar data based on NPKM, NPK and 'O' fertilization.

2 Values for quality characteristics measured for the allelic response of chromosome 1B and 1D according to Randall *et al.* (1993).

3 Flour yield based on the Quadrumat method.

TABLE 5.5 Effects of fertilization treatment on grain protein yield, grain protein content and flour yield of wheat (mean data from cultivars SST 86, Inia and Kariega)

Treatment	Grain protein yield (kg ha^{-1})	Grain protein content (dry basis) (%)	Flour yield[2] (%)
NPKM[1]	898c[+]	13.8c	50.8b
NPK	854c	13.3c	52.7bc
PK	473b	9.7a	49.2ab
NP	366b	10.9b	48.2ab
NK	156a	11.9b	54.4c
'O' Control	143a	10.4b	46.6a
CV %	23.9	6.9	12.0

\+ Within columns, means followed by the same lowercase letter had $P > 0.05$ and hence were not significantly different according to an Duncan's multiple range test.

1 Data based on cultivars SST 86, Inia and Kariega.

2 Flour yield based on Quadrumat method.

TABLE 5.6 Effects of cultivar on bread-making quality characteristics of two South African wheat cultivars

Cultivar	Loaf-volume[2] (cm^3)	Mixograph water absorption (%)	Mixograph peak mixing time (min)	Dough characteristics
Inia	910a[+]	62.5a	3.68a	Normal
Kariega	981b	62.2a	3.55a	Normal
CV %	1.3	1.5	3.5	

+ Within columns, means followed by the same lowercase letter had P > 0.05 and hence were not significantly different according to Duncan's multiple range test.

1 Bread-making quality data based on NPK, PK, NP and NK fertilization treatments only.

2 Based on breeder's standard 100 g loaf size.

Effect of soil fertility status
Grain protein yield

The main effect of soil fertility on grain protein yield is shown in Table 5.5. The NPKM treatment resulted in the highest grain protein yield (898 kg protein ha^{-1}), while the control '0' fertilization and NK treatments were the lowest and ranging from 143 to 156 kg protein ha^{-1}. In general, grain protein yield increased with increasing soil fertility although not all the differences were significant ($P > 0.05$).

Grain protein content

Grain protein content differed significantly with soil fertility status (Table 5.5; Appendix Tables 9.A9 and 9.A10). The NPKM treatment resulted in the highest grain protein content averaging 13.8% but did not differ significantly from the NPK treatment, while the PK treatment had the lowest at 9.7%.

In general, plots which received unbalanced soil nutrient treatments resulted in decreased protein content levels, showing the dependence of grain protein content on well-balanced soil nutrient status. The treatment generally lacking in N (PK treatment) resulted in the lowest grain protein level.

Flour yield

Flour yield differed significantly between the different soil fertility treatments (Table 5.5), with the NK treatment resulting in the highest flour yield (54.4%), while the control '0' treatment was the lowest averaging 46.6%.

The NPKM, NPK, PK and NP treatments varied slightly but did not differ in flour yield. In general, flour yield did not follow any definite pattern with increasing soil fertility status.

Bread-making quality

Loaf volume

Loaf volume differed with soil fertility as shown in Table 5.7. The NPK treatment, representing a well-balanced soil fertility situation averaged a volume of 988 $cm^{3,}$ while the PK treatment, in which soil N was limiting, averaged 880 cm^3. In the NPK treatment representing a well-balanced soil fertility situation, Kariega's loaf volume averaged 1025 cm^3 while Inia had 950 cm^3 of loaf volume (Appendix Table 9.A10).

Mixograph water absorption, mixograph mixing time and dough characteristics

Mixograph water absorption differed significantly with varying soil fertility status but not mixograph peak mixing time (Table 5.7). Water absorption was highest in the well-balanced NPK soil fertility treatment averaging 63.3%, and lowest (61.2%) in the N limiting soil fertility situation (PK treatment). As shown in Figures 5.2 and 5.3, comparison of mixograms of the two wheat cultivars tested show similar bread-making potential in all four soil fertility treatments with the exception of PK treatment (N limiting plots) which resulted in low protein content, low loaf volume and poor mixograph.

TABLE 5.7 Effects of soil fertility status on bread-making quality characteristics based on two South African wheat cultivars (mean data from cultivars Inia and Kariega)

Treatment	Loaf volume[1] (cm^3)	Mixograph water absorption (%)	Mixograph peak time (min)	Dough characteristics
NPK[2]	988c[+]	63.3d	3.5a	Normal
PK	880a	61.2a	3.8a	Normal
NP	980c	62.2b	3.6a	Normal
NK	935b	62.6c	3.8a	Normal
CV %	1.3	1.5	3.5	

\+ **Within columns, means followed by the same lowercase letter had P > 0.05 and hence were not significantly different according to Duncan's multiple range test.**

1 **Loaf-volume based on breeder's standard 100g loaf size.**

2 **Fertilization treatments NPK, PK, NP and NK (N - nitrogen; P - phosphorus; K - potassium).**

In general, increased soil fertility tended to decrease mixograph peak mixing time. Dough characteristics were not affected by less favourable soil fertility situations (Table 5.7).

Cultivar and soil fertility interaction

Grain protein yield

A significant interaction between cultivar and soil fertility was observed for protein yield, indicating cultivar differences in protein yield under differing soil fertility situations, particularly in soils low in N, K and P (PK, NP and NK treatments) as shown in Figure 5.1A. The cultivars generally reacted similarly except in NP and NPK treatments where Kariega performed better than the other cultivars producing the highest grain protein yield. In general, grain protein yield varied with cultivar and increased with increasing soil fertility.

Grain protein content

The cultivar and soil fertility interaction was significant for protein content indicating differential cultivar response in grain protein content to varying soil nutrient situations (Figure 5.1B). The interaction was due to SST 86 having the highest protein content in NK treatment plots and Inia the lowest, while in NP treatment plots, Kariega had the highest and Inia the lowest grain protein content.

Flour yield

The significant interaction between cultivar and soil fertility for flour yield shows differential cultivar performance mainly in P and K soil limiting situations (NK and NP treatments), as illustrated in Figure 5.1C.

Loaf volume

The significant interaction between cultivar and soil fertility observed for loaf volume was due to the differential increase and decrease in loaf volume in the PK, NP and NPK treatment plots (Figure 5.1D). Kariega produced larger loaves than Inia, but grain from the PK plots where nitrogen supply was limited resulted in similar sized loaves.

Mixograph water absorption, peak mixing time and dough characteristics

Significant interaction between cultivar and soil fertility was observed for mixograph water absorption (Figure 5.1E), but not for mixograph peak mixing time indicating cultivar differences in water absorption under varying soil fertility situations. This was mainly due to the fact that

Kariega flour from the PK-plots (Nitrogen limiting) exhibited poor absorption characteristics. (Figures 5.2 and 5.3)

5.5 DISCUSSION

High grain protein content has long been associated with good bread-making quality, and for a specific cultivar an increase in grain protein content normally results in increases in water absorption, loaf volume and general bread-making quality potential (Tipples, Dubetz & Irvine, 1977). In this investigation differences in the bread-making quality of the wheat cultivars under varying soil fertility situations were demonstrated, although differences in loaf volume could not be explained by differences in protein content levels only. Finney & Barmore (1948) studied US hard winter and spring wheats and found that the relation between grain protein content and loaf volume was linear.

In this study, the cultivar Carina had the highest protein yield and grain protein content but was lower in flour yield. The cultivars SST 86, Inia and Kariega did not differ in grain protein yield and grain protein content but varied in flour yield.

Grain protein yield generally increased with increasing soil fertility from the '0' Control and NK treatments to NP, PK, NPK and NPKM treatments. The high grain protein content obtained under conditions of well-balanced nutrient situations (NPK and NPKM treatments) compared to plots which generally were limited in N (PK treatment) showed that grain protein content was affected by both cultivar and soil nitrogen status (Tables 5.4 and 5.5).

The relatively high grain protein yield and grain protein content levels obtained can partly be attributed to soybean (*Glycine max*. L.), a nitrogen fixing legume, grown in rotation with wheat plots during the summer season.

The significant interactions between cultivar and soil fertility observed for protein yield and grain protein content indicated that the cultivars SST 86 and Inia reacted similarly to varying soil fertility. The good performance by Kariega in both P and K limiting soil fertility situations (NK and NP treatments) requires detailed investigation (Figure 5.1A, 5.1B and 5.1C).

The results show that for both Inia and Kariega grain protein content was positively correlated (P > 0.05) with loaf volume ($r^2 = 0.65$) as was evident in plots in which N was continuously applied (NK, NP, NPK and NPKM treatments).

Decreased grain protein content and loaf volume in N limiting plots (PK treatment) indicated the influence of N on grain protein content and loaf volume (Figures 5.1B and 5.1D). Figures 5.2 and 5.3 show that the cultivars reacted similarly to varying soil fertility situations, but for Kariega, in PK treatment, which showed reduced water absorption (%) compared to Inia (Figure 5.1E), probably due to its significant decrease in grain protein content. The high loaf volume produced by Kariega was unexpected but may be due to cultivar characteristics other than grain protein content level. The two wheat cultivars studied, however, produced good and comparable flours under varying soil fertility situations.

These results are in agreement with those of Dubetz (1972) who showed that, on irrigated land, grain protein content is usually increased with increments of N.

The same author reported that very high grain protein content was consistently obtained by controlled nutrient and moisture supply in Neepawa wheat grown on a field scale. Bushuk *et al.* (1978) and Rodriquez-Bores & Bushuk (1975) reported that when Neepawa wheat was grown under different fertilizer levels to produce grains varying in protein content from 9.6% to 16.9%, grain protein content was positively correlated with indices of bread-making quality. Similarly, Petrakora, Domanevskaia & Bredikhin (1974) found that gluten content and quality improved with increasing N application. Stoddard & Marshall (1990) found that most variation in protein content was environmental, although the genetic component was also significant.

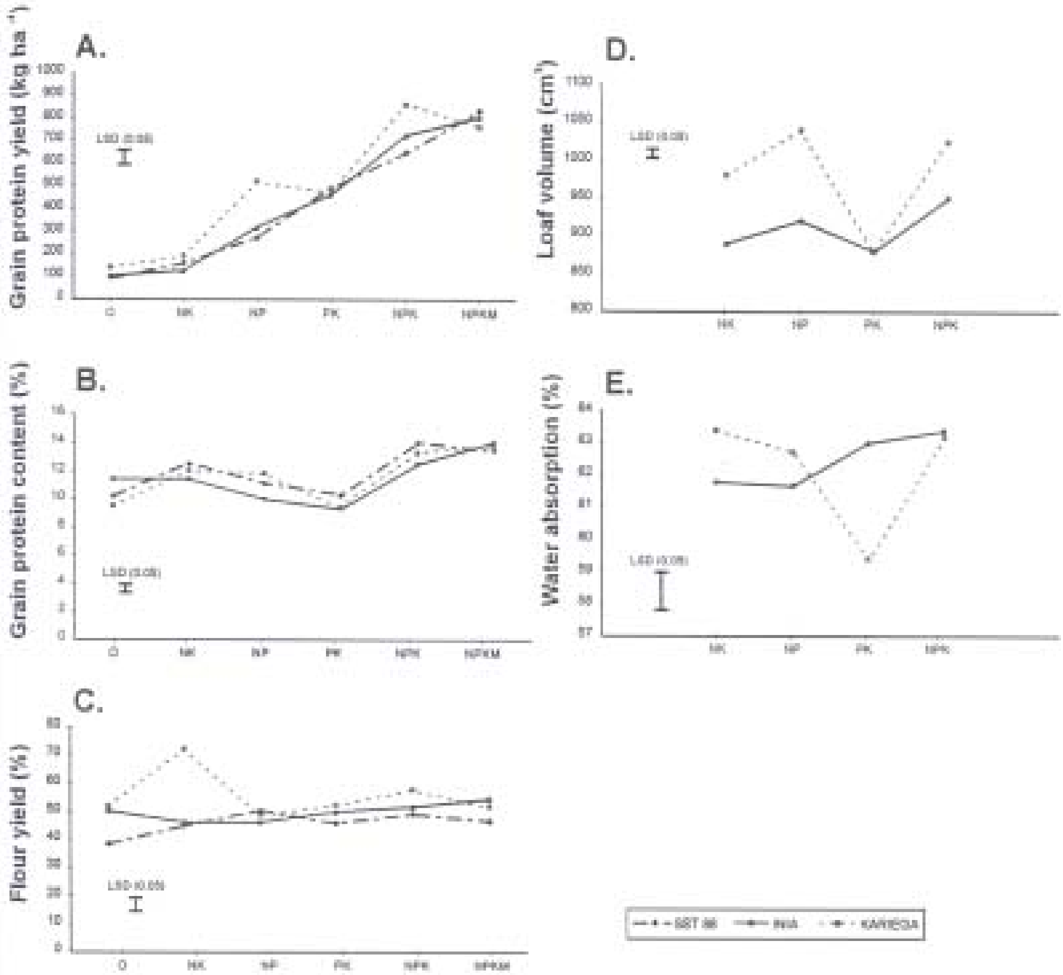

FIGURE 5.1 Interaction between cultivar and soil fertility on grain protein yield (A), grain protein content (B), flour yield (C), loaf-volume (D) and mixograph water absorption (E) of three South African wheat cultivars.

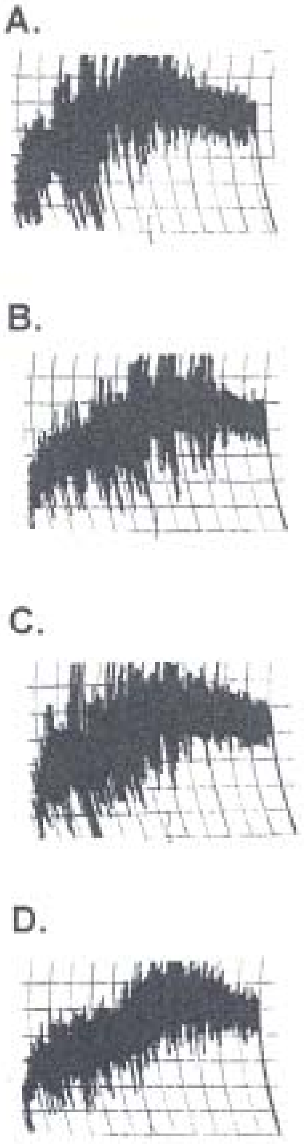

FIGURE 5.2 Response (mixograms) of wheat cultivar Inia to NPK(A), PK(B), NP(C)and NK(D) fertilization.

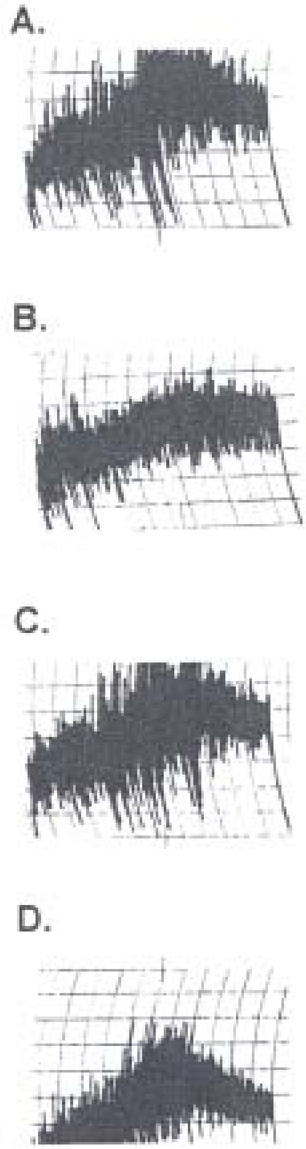

FIGURE 5.3 Response (mixograms) of wheat cultivar Kariega to NPK(A), PK(B), NP(C) and NK(D) fertilization.

Increasing attention is being focused on the possible role that certain high-molecular weight subunits of glutenin (HMW-GS) play in determining bread-making quality of wheats (Law & Payne, 1983). Randall *et al.* (1993) carried out a comprehensive study of the HMW-GS patterns of 38 South African bread wheat cultivars grown extensively in the past 15 years and reported that specific band patterns of HMW-GS were significantly correlated with end use quality, and were as good as rheological analysis in predicting loaf volume.

5.6 CONCLUSIONS

Under the conditions of this experiment, a correlation analysis showed that grain protein yield and grain protein content accounted for 65% of the variation in loaf volume. It was observed that cultivars with high grain protein content (%) were high protein yielders as well. This is in agreement with other studies which have reported the existence of wheat genotypes with both enhanced protein content and grain yield (Cox *et al.,* 1985; Löffler & Busch, 1982; Van Lill & Purchase, 1994). Thus on the basis of parameters of grain quality studied the cultivars varied significantly, although differences in loaf volume could not be adequately explained from the point of view of grain protein content only. Randall *et al*. (1993) reported that the Glu-1 scores, which are the sum of scores for the individual HMW-GS were the same (Table 5.4), except for differences in HMW-GS combinations. In this study, the effects of varying soil fertility on some of the grain quality characteristics were quantified, and the hypothesis that wheat genotype and soil fertility affect bread-making quality was proven. We hypothesize that the high loaf volume potential of the cultivar Kariega was probably genetical and may be due to factors other than grain protein content level which require detailed investigation.

The data indicate that soil fertility affects loaf volume, but differences in loaf volume between cultivars could not be explained solely by protein content level. Grain protein content was, however, associated with bread-making quality.

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CHAPTER 6

INFLUENCE OF SOIL FERTILITY AND CULTIVAR ON LEAF AREA INDEX AND BIOMASS PRODUCTION

6.1 ABSTRACT

Total dry matter production is a good indicator of the degree of adaptation of a wheat (*Triticum aestivum* L.) genotype to the environment in which it is being grown. The objective of this study was to determine the effects of soil fertility and wheat genotype on leaf area index (LAI), aboveground biomass accumulation and ear:vegetative dry-mass ratio. Four wheat cultivars (Inia, Carina, Kariega and SST 86) were planted in a split-plot design in a randomized complete block and replicated four times with six fertility treatments as main plots, and the cultivars as the sub-plots using the long-term fertilization and irrigation experiment, at Hatfield Experimental Farm of the University of Pretoria. The cultivars differed significantly in biomass at terminal spikelet formation, 50% flowering and at maturity but did not differ in leaf area index (LAI). The aboveground biomass at maturity was highly correlated (r^2 = 0.85) with the final grain yield but poorly correlated (r^2 = 0.34) with maximum LAI. At anthesis Carina had the largest mean biomass averaging 9.1 t ha^{-1} with a LAI of 4.3 and SST 86 the lowest at 5.6 t ha^{-1} with a LAI of 4.0. Leaf area duration (LAD) was longest for Kariega and shortest for SST 86. Carina had the highest ear dry-mass, averaging 8.1 t ha^{-1} and SST 86 produced lowest ear dry-mass (4.8 t ha^{-1}) while Kariega was intermediate (6.2 t ha^{-1}). Vegetative dry-mass was highest for Carina (7.2 t ha^{-1}) and did not differ between SST 86, Inia and Kariega ranging from 3.5 to 4.9 t ha^{-1}. The cultivar SST 86 had the highest ear:vegetative ratio (1.4:1) but was lower in grain yield, while Carina had the lowest ratio (0.89:1) but produced higher grain yield. Leaf area index and biomass increased with increasing soil nutrient status. Significant interactions between soil fertility and cultivar were observed for ear dry weight and aboveground biomass but not for leaf area index. These results indicate cultivar differences in ability to produce and allocate dry-mass to the ear. Under the experimental conditions, biomass accumulation was positively correlated (r^2 = 0.85) with cultivar grain yield.

Key words: Biomass yield, leaf area index, soil nutrient status, *Triticum aestivum* L.

6.2 INTRODUCTION

The amount of photosynthate available for biomass production is related to the current leaf area and the photosynthetic rate of the crop in consideration (Meyer & Green, 1980; Muldoon, Daynard, Van Duinen & Tollenaar, 1984). As biomass accumulation is dependent on the absorbed photosynthetically active radiation (PAR), the total amount of biomass will be affected by the canopy developed (Black, 1963). Several studies on the relationship between leaf area and biomass accumulation have been reported (Watson, 1937, Watson, Thorne & French, 1963; Zrust, Partykova & Necas, 1974). Aase (1977) reported a high correlation between leaf area and dry weight in annual crops. In crop modelling leaf area indices are needed (Marshalls, 1968; Aase, 1975; 1978), and biomass production may be substituted for leaf area index. Blackman (1956) indicated that the leaf area to leaf dry matter relationship may change during plant growth and with environmental conditions. Unfavourable temperature conditions, water stress or inadequate soil fertility during the early stages of leaf growth will result in a large reduction in maximum leaf area attained by the crop (Bradford & Hsiao, 1982). Annandale, Hammes & Nel (1987) reported a significant correlation (r^2 = 0.69) between maximum leaf area index and aboveground dry matter accumulation under varying soil nutrient status of wheat.

Grain yield of wheat has been analysed in relation to total biomass produced and its partitioning into yielding organs. Biscoe (1979) & McLeran (1981) reported that biomass production is linearly related to final grain yield, is proportional to the amount of solar radiation intercepted by the foliage, is related to the canopy size, leaf arrangement and photosynthetic efficiency. Canopy size is affected by husbandry and climate (Gallagher & Biscoe, 1978) while leaf arrangement may be affected by applications of growth regulating chemicals (Roebuck, 1981) and by plant breeding (Innes & Blackwell, 1983).

Fertilization, especially with nitrogen (N), can influence tillering and final size of individual leaves, leaf area and hence, leaf area index. The efficiency of conversion of absorbed radiation into dry-matter of temperate cereals can be reduced by nutrient deficiencies or water stress (Cock & Yoshida, 1973; Biscoe, Scott & Monteith, 1975). At a given site there may be little variation in incident radiation between seasons, but distinct differences in production of biomass may occur in regions at different latitudes. As the fraction of carbon respired is often a constant fraction of carbon fixed (Cock & Yoshida, 1973; Biscoe & Willington, 1984), conversion efficiency will be related to canopy photosynthetic rate, and hence to the amount of biomass produced. Understanding the effects of soil fertility and wheat genotype on leaf area development and leaf area duration in relation to biomass accumulation and distribution is important, and may result in information beneficial to manipulating source-sink relationships between the yielding organs to improve wheat yield.

The main objectives of this study was to quantify the leaf area and hence leaf area index, aboveground dry biomass and ear:vegetative dry-mass ratio of four South African wheat (*Triticum aestivum* L.) cultivars, over a range of different soil fertility situations.

6.3 MATERIALS AND METHODS

Details of the experimental treatments are presented in Chapter 2. Leaf area index and aboveground biomass accumulation were determined at terminal spikelet (TS) stage, booting stage and 50% anthesis. Dry-mass was also measured at physiological maturity.

Site, soil and crop husbandry practices

Details of experimental site, soil, husbandry and cultural practices were described by Nel, Barnard, Steynberg, de Beer & Groeneveld (1996). The experimental treatments, design, layout, plot dimensions, weather for 1995, pH, site soil analysis and statistical procedure followed are described in detail by Metho, Hammes, De Beer & Groeneveld (1997) and Chapter 3.

Data recorded

At terminal spikelet (TS) stage, heading stage and 50% anthesis plants were sampled from a 1.0 by 0.9 m area starting from time of 50% emergence, and leaf area index and biomass determined. Leaf area index was determined from a 1 m row of plants, using a LI 3100 leaf area meter. The weight of each dry-matter sample in g m^{-2} was determined after oven drying to a constant moisture content at 60 ^{0}C for 72 hours. To cause minimum interference with long-term rotation practice only treatments NPKM, NPK and Control '0' were retained for determination of leaf area index, biological yield and dry-mass yield in the case of the late maturing Carina.

6.4 RESULTS

The main effects of soil fertility and cultivar on leaf area index, biomass and ear:vegetative dry-mass ratio are shown in Tables 6.1, 6.2, 6.3, 6.4 and 6.5. Significant soil fertility and cultivar interactions on ear dry-mass and straw dry-mass are illustrated in Figures 6.1 and 6.2. The main effects of cultivar and soil fertility on grain yield, yield components and significant interactions are reported in Chapter 3.

Leaf area index (LAI)

Main treatment effects

Effect of soil fertility

Leaf area index data are presented in Tables 6.1 and 6.2 for the terminal spikelet stage and the heading stage, respectively. At the terminal spikelet stage leaf area index differed significantly with varying soil nutrient treatment. Treatment NPKM produced the largest mean leaf area index averaging 5.1. The NP and NK treatments resulted in low leaf area indices (0.79. The NPK and PK treatments were intermediate and differed significantly with leaf area indices of 3.8 and 1.5 respectively. No leaf area index data for the unfertilized control treatment '0' is available.

Table 6.2 shows the NPKM treatment had the highest leaf area index at heading (6.8) while the Control '0' and NK treatments were lowest. For the treatment NPK the leaf area index averaged 5.5 and was significantly different from the other treatments (Table 6.2). In general the well-balanced soil nutrient treatments (NPKM and NPK) resulted in higher leaf area indices than the unbalanced soil fertility situations (e.g. PK, NP and NK treatments).

Effect of cultivar

Leaf area index data are presented in Tables 6.1 and 6.2. The cultivars did not differ in leaf area index at the terminal spikelet stage ranging from 2.2 to 2.8 (Table 6.1), but differed significantly at the heading stage (Table 6.2). Carina produced the highest leaf area index (3.6) and SST 86 the lowest (2.9). Inia and Kariega were intermediate in leaf area index ranging between 3.2 to 3.3 (Table 6.2). Leaf area duration (LAD) was observed to be longest for Kariega and shortest for SST 86 (data not shown).

TABLE 6.1 Effect of fertility on leaf area indices at terminal spikelet stage of four South African cultivars

Treatment		CULTIVAR				
		SST 86	Inia	Kariega	Carina	Mean
Fertility	NPKM	4.9c	5.2d	4.6c	5.7e	5.1d
	NPK	4.2c	4.0c	3.9c	3.2d	3.8c
	PK	1.5b	1.8b	1.6b	1.3b	1.5b
	NP	1.8b	1.8b	1.9b	2.4c	0.79a
	NK	0.80a	0.96a	0.64a	0.75a	0.79a
Mean		2.6a	2.8a	2.2a	2.7a	

Means within columns followed by the same letter are not significantly different according to Fisher's test (P ≤ 0.05). Each value is a mean of 18 observations.

TABLE 6.2 Effect of soil fertility on leaf area indices at heading of four South African cultivars

Treatment		CULTIVAR				
		SST 86	Inia	Kariega	Carina	Mean
Fertility	NPKM	6.4d	7.5b	6.8d	6.4d	6.8d
	NPK	5.0c	5.5c	5.1c	6.4d	5.5c
	PK	2.3b	2.3b	2.7b	3.8c	2.8b
	NP	2.4b	2.6b	2.7b	2.7b	2.6b
	NK	0.96a	1.1a	0.79a	1.1a	0.99a
	'O' Control	0.68a	0.89a	1.1a	0.85a	0.88a
Mean		2.9a	3.3ab	3.2ab	3.6b	

Means within columns followed by the same letter are not significantly different according to Fisher's test (P ≤ 0.05). Each value is a mean of 18 observations.

TABLE 6.3 Effect of soil fertility on cultivar aboveground biomass yield at terminal spikelet stage of four South African wheat cultivars

Treatment		BIOMASS YIELD (t ha^{-1}) CULTIVAR				
		SST 86	Inia	Kariega	Carina	Mean
Fertility	NPKM	5.9c	5.5c	6.3c	14.3e	7.9d
	NPK	5.7c	7.3d	7.4c	9.0d	7.4d
	PK	5.1c	4.3b	4.9b	5.8c	5.0c
	NP	2.4b	4.7b	3.9b	3.9b	3.7b
	NK	1.6a	1.7a	1.8a	1.6a	1.7a
Mean		4.8a	4.7a	4.8a	6.9b	

TABLE 6.4 Effect of soil fertility on cultivar aboveground biomass yield at anthesis of four South African wheat cultivars

Treatment		BIOMASS YIELD (t ha^{-1}) CULTIVAR				
		SST 86	Inia	Kariega	Carina	Mean
Fertility	NPKM	9.3d	11.6d	15.6e	15.6c	13.0e
	NPK	8.3cd	9.2c	12.7d	11.3bc	10.4d
	PK	6.9c	6.6b	10.1c	10.6b	8.6c
	NP	4.1b	6.2b	7.2b	9.6b	6.8b
	NK	2.8a	3.3a	4.4a	3.7a	3.6a
	‘O’ Control	2.3a	3.8a	3.4a	3.9a	3.4a
Mean		5.6a	6.8b	8.9c	9.1c	

Means within columns followed by the same letter are not significantly different according to Fisher’s test ($P \leq 0.05$). Each value is a mean of 18 observations.

All four wheat cultivars reacted similarly producing higher leaf area indices in the well-balanced soil fertility situations (NPKM and NPK treatments) and were lower in the unbalanced or unfertilized plots (Tables 6.1 and 6.2).

Biomass yield

Effect of soil fertility

The aboveground biomass yields are presented in Tables 6.3 and 6.4 for the terminal spikelet stage and at anthesis respectively. Biomass yield differed significantly with soil nutrient status and with stage of development. The balanced NPKM and NPK treatments produced higher biomass varying from 6.9 to 6.4 t ha^{-1}. The NK treatment resulted in the lowest biomass (1.7 t ha^{-1}) (Table 6.3). PK and NP treatments were intermediate but differed significantly in biomass yield, averaging 5.0 and 3.7 t ha^{-1} respectively at the terminal spikelet stage. No data is available for the control '0' treatment.

At anthesis the NPKM treatment produced the largest biomass yield (13.0 t ha^{-1}) while the treatments NK and control 'O' were lowest. The NPK treatment produced significantly more biomass (10.4 t ha^{-1}) than PK (8.6 t ha^{-1}) and NP (6.8 t ha^{-1} (Table 6.4).

Table 6.5 shows that dry-matter production differed significantly at physiological maturity, with the well-balanced soil fertility treatments NPK and NPKM ranging from 15.9 to 16.3 t ha^{-1} respectively, and the control "0" treatment ranked the lowest (4.7 t ha^{-1}). Because Carina data in the PK, NP and NK treatments are not available the treatment means refer to the cultivars SST 86, Inia and Kariega and hence, no comparison is made other than that for treatments NK, NP and PK dry-matter yields varied from 4.3, 9.0 to 12.0 t ha^{-1} (Table 6.5).

Effect of cultivar

The results of the biomass yield at the terminal spikelet stage and at 50% anthesis are shown in Tables 6.3 and 6.4, respectively. At the terminal spikelet stage Carina produced the largest biomass (6.9 t ha^{-1}) with SST 86, Inia and Kariega biomass yields significantly lower, ranging from 4.7 to 4.8 t ha^{-1} (Table 6.3). At anthesis (Table 6.4) Carina and Kariega did not differ in their biomass yield of approximately 9 t ha^{-1}, while SST 86 had the lowest biomass of 5.6 t ha^{-1}. Inia was intermediate with a biomass yield of 6.8 t ha^{-1}, but was significantly different from SST 86 and Kariega (Table 6.4).

TABLE 6.5 Effect of soil fertility on cultivar aboveground dry matter at maturity of four South African wheat cultivars

Treatment		DRY MATTER (t ha^{-1}) CULTIVAR				
		SST 86[1]	Inia[1]	Kariega[1]	Carina[2]	Mean
Fertility	NPKM	14.0e	15.5d	14.8c	20.8b	16.3b
	NPK	12.2d	14.5d	16.3d	20.5b	15.9b
	PK	10.9c	12.4c	12.8b	-	(12.0)
	NP	6.3b	8.7b	12.1b	-	(9.0)
	NK	4.1a	4.0a	4.7a	-	(4.3)
	'O' Control	3.6a	3.0a	4.5a	7.7a	4.7a
Mean		8.5a	9.7b	10.9c	16.3d	

Means within columns followed by the same letter are not significantly different according to Fisher's test ($P \leq 0.05$). Each value is a mean of 18 observations.

1 Cultivar means based on six soil fertility treatments NPKM, NPK, PK, NP, NK and 'O' Control.

2 Cultivar mean based on three soil fertility treatments NPKM, NPK and 'O' Control.

The four wheat cultivars differed in dry-matter production at physiological maturity. Averaged over the NPKM, NPK and Control '0' treatments, Carina had the highest (16.3 t ha^{-1}) and SST 86 the lowest (8.5 t ha^{-1}) biomass (Table 6.5). Inia and Kariega were intermediate but differed significantly.

In general the highest dry-matter was produced under conditions of balanced soil fertility status (NPKM and NPK treatments) and was drastically reduced in the nutrient limiting soil situations (PK, NP, NK and Control '0' treatments (Table 6.5).

Ear:vegetative dry-mass ratio

The ear:vegetative dry-mass ratio's are presented in Tables 6.6 and 6.7 show the NPKM, PK and NP treatments averaged 1:3, and treatments NK and Control '0' averaged 1:1. The cultivars, however, differed with SST 86 having the highest ratio (1.4:1) but with significantly lower dry-matter yield, and Carina the lowest (0.89:1) and having the highest dry-matter yield (Tables 6.6 and 6.7). Inia and Kariega were intermediate (1.1:1 vs 1.3:1, respectively) (Table 6.7). In general ear and vegetative dry-mass yields, and ear:vegetative dry-mass ratio increased with increasing soil fertility situation from the Control 'O' treatment to the NPKM treatment (Table 6.6).

Interaction between soil fertility and cultivar on biomass yield, ear and straw dry-mass production

Significant interactions between soil fertility and cultivar were observed for aboveground biomass at terminal spikelet stage and at physiological maturity (Figures 6.1, 6.2 and Chapter 2, Figure 2.2). P resulted in the highest total aboveground biomass (9.4 t ha^{-1}) compared to K (6.9 t ha^{-1}) and N (4.4 t ha^{-1}) at anthesis stage.

Significant interactions between soil fertility and cultivar observed for ear and vegetative dry-mass yields (Figures 6.1, 6.2 and Chapter 2, Figure 2.5) indicated differential cultivar accumulation of ear and vegetative dry-mass with varying soil nutrient status. Figure 6.1 shows that the cultivars reacted similarly in ear dry weight to the P limiting (NK treatment) soil fertility situation, but differed significantly in the N and K limiting (PK and NP treatments) showing a cross-over interaction effect.

The wheat cultivars again reacted similarly to N, P and K soil limiting fertility situations (Figure 6.2). In the P soil limiting (NK treatment) the cultivars did not differ but in the K soil limiting situation (NP treatment) Carina had the highest vegetative dry-mass yield and SST 86 the lowest (Figure 6.2).

The interaction between soil fertility and cultivar was not significant for leaf area index at terminal spikelet stage and heading stage, respectively.

TABLE 6.6 Effect of soil fertility dry mass of ears and vegetative parts and growth ratio of four South African wheat cultivars at final harvest

Treatment		DRY MATTER (t ha^{-1})		
		Ear	Stem and vegetative parts	Ear: Vegetative parts ratio
Fertility[1]	NPKM	8.6c	6.9c	1.3 : 1
	NPK	7.5c	6.4c	1.2 : 1
	PK	6.7b	5.3b	1.3 : 1
	NP	5.2b	3.8b	1.3 : 1
	NK	2.3a	2.0a	1.1 : 1
Control	'O'	2.0a	1.9a	1.1 : 1
	LSD_T $P_{\leq 0.05}$	1.4	1.7	
Mean		5.4	4.4	1.2 : 1
CV%		16.5	19.3	

Significant at P ≤ 0.05.
1 Fertility data based on cultivars SST 86, Inia and Kariega Carina.

TABLE 6.7 Effect of cultivar on ear: vegetative growth ratio of four South African wheat cultivars at final harvest

Treatment		DRY MATTER (t ha^{-1})		
		Ear	Stem and vegetative parts	Ear : Vegetative parts ratio
Cultivar[2]	SST 86	4.8a	3.5a	1.4 : 1
	Inia	5.1ab	4.8a	1.1 : 1
	Kariega	6.2b	4.9b	1.3 : 1
	Carina	8.1c	7.2c	0.89 : 1
	LSD_T $P_{\leq 0.05}$	1.2	1.1	
CV%		16.5	19.3	

Significant at P ≤ 0.05.
1 Cultivar data based on fertility treatments NPKM, NPK and Control 'O' only.

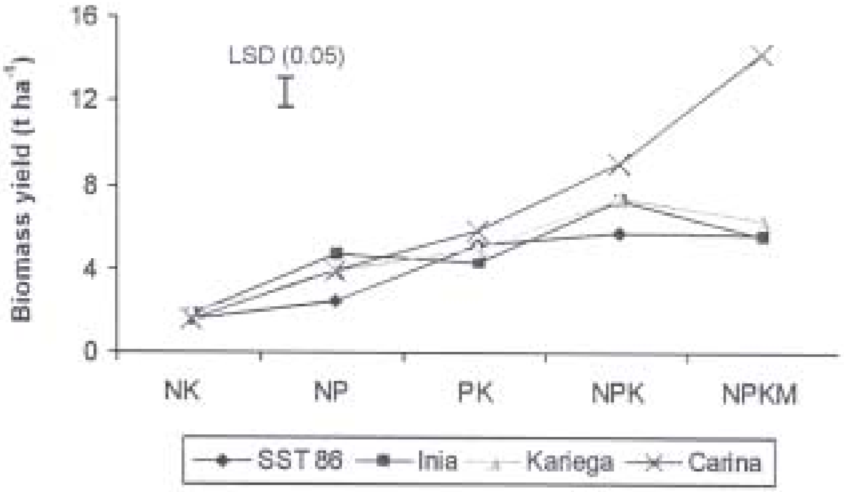

FIGURE 6.1 Interaction between soil fertility and cultivar on biological yield of four South African wheat cultivars at terminal spikelet stage.

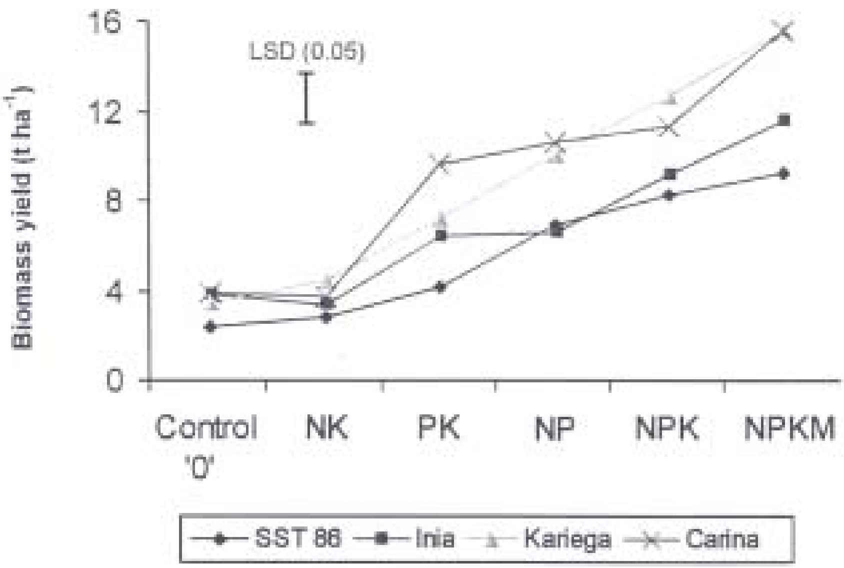

FIGURE 6.2 Interaction between soil fertility and cultivar on biological yield of four South African wheat cultivars at 50% anthesis.

6.5 DISCUSSION

Total dry-matter production is a good indicator of the degree of adaptation of a wheat plant to the environment in which it is being grown, while grain yield has been analysed in relation to total biomass produced and its partitioning into yielding organs. For example, leaf area and hence, leaf area index attained, determines the amount of photosynthate available for biomass production. Leaf area index is influenced by cultivar, leaf arrangement, photosynthetic rate and efficiency, solar radiation intercepted by the foliage, husbandry, climate and soil fertility (Gallagher & Biscoe, 1978; Biscoe, 1979; Meyer & Green, 1980; Muldoon *et al*., 1984; Walker, 1988). Any of these factors may seriously affect biomass production and final grain yield. As total amount of biomass will be affected by a crop's canopy developed, understanding of the effects of soil fertility and cultivars on leaf area index and biomass accumulation and partitioning may result in management strategies for maximizing yield and in cultivar selection for specific wheat growing environments.

The data indicated that leaf area index and aboveground biomass was increased significantly in the well-balanced soil fertility situations. The cultivars, however, differed significantly in biomass yield, ear dry weight and straw dry-mass, but not in leaf area index (Tables 6.1 and 6.2). Soil nutrient imbalances caused large reductions in both leaf area index and final dry-matter produced, depending on whether P, K or N was the most limiting soil nutrient.

Under the experimental conditions, the aboveground biomass was better correlated ($r^2 = 0.85$) with grain yield than with leaf area index ($r^2 = 0.34$). The results agree with those of Biscoe (1979) and McLeran (1981) who reported that biomass was linearly related to final grain yield. Fertilization, especially with N, can influence tillering and final size of individual leaves and number, hence, leaf area index. The efficiency of conversion of absorbed radiation into dry-matter can be reduced by severe soil fertility deficiencies (Cock & Yoshida, 1973; Biscoe *et al*., 1975). Annandale, Hammes & Nel (1987) reported a significant correlation ($r^2 = 0.69$) between maximum leaf area index and aboveground dry-matter accumulation at maturity.

The competitive relationship between the ear and the stem is thought to determine floret survival and hence grain number per spikelet and per ear in wheat. Other studies have shown that the higher yield of modern varieties is related to higher harvest indices, and that there has been little change in total biomass (Jain & Kulshrestha, 1976; Austin, Bingham, Blackwell, Evans, Ford, Morgan & Taylor, 1980; Siddique, Kirby & Perry, 1989). In terms of yield components, per-grain dry-matter has been found to be relatively stable and increases in yield have been associated with increase in number of grains per ear or per unit area (Brooking & Kirby, 1981; Fischer & Stockman, 1986; Perry & D'Antuono, 1989).

In this investigation differences in leaf area index, aboveground biomass production and ear:vegetative dry-mass ratio over a wide range of soil fertility situations were quantified. Under the experimental conditions, the results indicate that leaf area index and aboveground biomass increased with increasing soil fertility. Soil nutrient imbalances caused a large reduction in both the leaf area index attained and the amount of biomass produced.

The need for balanced fertilization for efficient utilization of applied nutrients is demonstrated by the higher biomass yield of treatments NPKM and NPK compared to the other treatments (PK, NP and NK) in which one of the macro-nutrients was limiting. Differences in ability to allocate dry-matter to the ear at maturity is indicative of differences in source-sink potential between the four wheat cultivars studied and may be partly responsible for the grain yield advantage of Carina over the other cultivars.

6.6 CONCLUSIONS

The results indicated that increasing soil fertility status increased leaf area index, biomass and final dry-matter yield at harvest, depending on wheat genotype.

The ear dry mass, straw dry-mass and ear:vegetative dry-mass ratio increased with increasing soil fertility. The biomass yield at anthesis and dry-matter at maturity were positively correlated (r^2 = 0.85) with the final grain yield but poorly (r^2 = 0.34) with leaf area index. Leaf area duration was observed to vary with nutrient status and cultivar.

Under the specif conditions of this long-term fertilization trial phosphorus (P) deficiency caused the greatest reduction in leaf area index and biomass yield, followed by potassium (K) and nitrogen (N), respectively. Balanced soil fertility treatments (NPKM and NPK plots) produced the highest leaf area index and the largest aboveground biomass and final dry-matter yield at maturity. This is to be expected as the healthy and strongly growing crops have a much larger photosynthetic factory to absorb maximum of incident radiation (PAR) and hence, the higher biomass yield. These results indicate cultivar differences in ability to produce and allocate dry-mass to the ear and hence grain yield potential.

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CHAPTER 7

EFFECTS OF PHOTOPERIOD AND TEMPERATURE ON GRAIN YIELD, GRAIN NUMBER, MEAN KERNEL MASS AND GRAIN PROTEIN CONTENT OF VERNALIZED AND UNVERNALIZED WHEAT

7.1 ABSTRACT

Wheat is grown under divergent climatic conditions in South Africa, varying from cool short days to warm long days. This affects yield and grain quality. The purpose of this study was to determine how photoperiod, temperature and vernalization affects wheat grain yield, components of yield and grain protein content. Vernalized and unvernalized seeds of four wheat cultivars (Inia, Carina, Kariega and SST 86) were studied in controlled growth chambers comprising two photoperiods and two temperature regimes (photoperiod 11 hr/temperature 20-15 ^{0}C; 13 hr/20-15 ^{0}C; 11 hr/15-5 ^{0}C and 13 hr/15-5 ^{0}C). Temperature treatments were applied on a 12 hr-12 hr basis. In the 13 hr/15-5 ^{0}C treatment the grain yield averaged 11.9 g per plant with a 18.5% grain protein content. In the 11 hr/20-15 ^{0}C treatment the yield averaged 1.7 g per plant and 12.4% protein content. The highest yielding cultivar, averaged over all environments, was Kariega yielding 7.5 g per plant, with SST 86 the lowest at 4.8 g per plant. Vernalized Inia and Kariega yielded between 14-25% higher depending on cultivar, but vernalized or unvernalized SST 86 and Carina did not differ in yield. The interactions of photoperiod and temperature; photoperiod and cultivar; photoperiod, temperature and cultivar were significant with respect to grain yield, grain number, mean kernel size and grain protein content. These results indicate that low temperature regimes (15-5 ^{0}C) and long photoperiod (13:11 hr) treatments resulted in the highest grain yield, number of grains, largest mean kernel size and higher grain protein content. Grain number was the most variable component of yield and kernel size varied the least. Understanding the cultivar and growth environment interaction is important for yield improvement in different climatic regions.

Key words: Grain protein content, photoperiod, *Triticum aestivum* L., temperature, vernalization, yield and components

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7.2 INTRODUCTION

When plants are exposed to longer daylengths and/or lower night temperatures, production is often improved through a balance between photosynthesis and respiration (Downs & Hellmers, 1975; Salisbury, 1979; Mitchell, Lawlor & Young, 1991). In South Africa, wheat (*Triticum aestivum* L.) is grown under widely divergent climatic conditions, varying from cool short days to warm long days (Nel & Small, 1973; Hammes & Marshall, 1980).

Understanding the reaction of local wheat cultivars to varying photoperiod and temperature conditions as manifested in the grain yield and grain quality can improve regional wheat yield and grain quality.

Several studies on the effects of photoperiod, temperature and vernalization of wheat have been reported, but few have analyzed the interactive effects between photoperiod, temperature and vernalization on yield and grain protein content (Wardlaw, 1970; Joubert & Laubscher, 1974; Warrington, Dunstone & Green, 1977; Hammes & Marshall, 1980). It is reported that the rate of development of a wheat ear was greater and final number of spikelets on the ear was less at higher temperatures (Warrington, Dunstone & Green, 1977). High spikelet numbers at low temperatures are due to a much longer period of spikelet differentiation (Friend, Fischer & Helson, 1963). Other writers have reported that at high temperature (30^0C) grain ripening was accelerated and this resulted in smaller grains at maturity (Hoshikawa, 1961; Midmore, Cartwright & Fischer, 1984). In studying four cultivars grown at three temperatures imposed during grain development it was found that grain yields were highest at low temperature and were associated with a longer period of grain growth (Sofield, Evans & Wardlaw, 1974). Similar results for various temperatures imposed during the grain growth stage have been reported by Spiertz (1974). Several writers have reported that flower induction of wheat exposed to longer days was hastened causing a reduction in spikelet number (Thorne, Ford & Watson, 1968; Rawson, 1970; Wall & Cartwright, 1974).

In South Africa wheat may be sown in spring, autumn or winter depending on the production area. Some local cultivars, including those grown in the Winter Rainfall Region, are spring wheats (Sim, 1965). In South Africa the term "summer wheat" is popularly used for wheat sown in spring or early summer while "winter wheat" is sown in autumn or early winter. Consequently, a vernalization requirement may be beneficial to allow sensitive wheat cultivars to delay flowering untill the end of the frost season. Spring wheat cultivars may also have marked vernalization responses which can be of advantage in delaying inflorescences and may increase the number of spikelets differentiated, and hence yield capacity (Rawson, 1970; Levy & Peterson, 1972). Vernalization temperatures can range between 0 ^{0}C to 11 ^{0}C (Gott, 1961; Aherns & Loomis, 1963). It has been reported that the optimum temperature was 11 ^{0}C for spring wheat and 3 ^{0}C for winter wheat (Junges, 1959).

The main objective of the trial reported in this chapter was to quantify the effects of two photoperiods and two temperatures on grain yield, yield components and grain protein content of four vernalized and unvernalized South African wheat cultivars grown under controlled growth environments.

7.3 MATERIALS AND METHODS

Photoperiod and temperature treatments

The experiment was conducted in four plant growth-chambers of the Controlled Environment PGW_{36} type at the Hatfield Experimental Farm, University of Pretoria. The irradiance over the course of the study at average plant height was 505-650 μEm^{-2} sec^{-1}, as measured by a Lambda Instruments Model LI 185 quantum meter.

The temperature treatments used were 20/15 ^{0}C and 15/5 ^{0}C day/night on a 12 hr - 12 hr basis. The photoperiod was 11:13 hr and 13:11 hr with an abrupt light/dark change, the lights coming on and going off half-way through the temperature/humidity change over. The vapour pressure deficits during the experiment were typically 10 mb by day and 4 mb by night.

Plant material and general procedure

Certified seed of four wheat cultivars Inia, Carina, Kariega and SST 86 were selected for uniformity and germinated on wet filter paper at laboratory temperature. Prior to the germination one lot of seeds were vernalized at 0 to -4 ^{0}C for 10 days after thorough soaking in distilled water for 12 hr. Eight pre-germinated seeds were planted per container of which four plants were allowed to grow to maturity. The 1 litre containers were filled with a coarse sand, peat and vermiculite (70:15:15 v/v) mixture and placed in the controlled growth chambers.

The containers were watered three times per week with nutrient solution (Nitsch, 1972), and flushed with a surplus of deionised water once weekly to prevent salt accumulation. Treatments were rotated twice during the study period to minimize the effect of possible differences, other than the treatments between the chambers. Despite the small containers vigorous growth occured and good yields were obtained.

Wheat cultivars

The cultivar Inia usually has a short growing period, is of medium height, and is grown in autumn, winter or spring in various parts of the country. Kariega is of medium height and intermediate maturity, and is recommended for irrigation areas. SST 86 is an early maturing semi-dwarf with strong straw strength. Neither of these cultivars has a definite cold requirement and is often grown in winter or spring in the summer rainfall areas. Carina is a hybrid, has a longer growing period and is tall-growing. Carina has a cold requirement and is extensively grown in the Free State, under dryland conditions and in the Eastern Gauteng Province where it is sown at the beginning of the winter.

Measurements

Plants were considered to be physiologically mature when the ears from secondary tillers contained no more chlorophyll, and were harvested as soon as they were dead. Grain yield, grain number, mean kernel mass, ear number and spike and straw dry mass was determined on a per plant and per pot basis (plant material was oven dried at 60 ^{0}C for 48 hr). Grain protein content was estimated from grain nitrogen measured by a Kjeldhal method (A.A.C.C., 1986 method 46-12, and protein as N X 5.7) (A.A.C.C., 1986).

Experimental design and statistical analysis

Treatments were arranged in a split-plot design with four replications. Photoperiod-temperature combinations were treated as the main plots, cultivars as the sub-plots and the vernalization treatments as the sub-subplots. Data was analyzed using the General Linear Models (GLM) procedure of the Statistical System (SAS Institute Inc. Cary, NC., USA 1989 Copyright) computer program. Differences at the $P \leq 0.05$ level of significance are reported. Tests of heterogeneity of variances for all characteristics were done and probabilities calculated according to Steel & Torrie (1980). Due to the missing or unbalanced nature of the data Fisher's test was performed.

7.4 RESULTS

The main effects of photoperiod, temperature, vernalization and cultivar on grain yield, grain number, mean kernel mass and grain protein content are shown in Tables 7.1, 7.3, 7.5 and 7.7. Significant interactions between photoperiod x temperature, photoperiod x cultivar, vernalization x cultivar, photoperiod x temperature x cultivar and photoperiod x vernalization x cultivar for grain yield, grain number, mean kernel mass and grain protein content are shown in Tables 7.2a-e, 7.4a-e, 7.6a-e and 7.8a-b.

Grain yield

Main treatment effects

Photoperiod significantly affected grain yield, with the 13:11 hr treatment yielding 7.2 g per plant and the 11:13 hr treatment averaging 5.0 g per plant (Table 7.1). Temperatures of 15-5 ^{0}C resulted in a significantly higher grain yield averaging 10.1 g per plant compared to 2.1 g per plant for the 20-15 ^{0}C temperature treatment (Table 7.1). Vernalization significantly increased grain yield, with plants from vernalized seed yielding 6.5 g per plant, and those from unvernalized seed averaged 5.7 g per plant (Table 7.1). Cultivar grain yield, averaged over all treatments, differed significantly with Kariega and Inia producing higher yields than SST 86 and Carina (Table 7.1)

TABLE 7.1 Effects of photoperiod, temperature and vernalization treatments on grain yield (g per plant) of four South African spring wheat cultivars in controlled growth chambers

Treatment	Photoperiod (hours)		Temperature (°C)		Vernalization		Cultivar Mean grain yield (g per plant)
	11:13	13:11	15-5	20-15	Vern.	Unvern	
Wheat Cultivar							
Inia	5.92b	8.18b	10.88c	3.22c	7.86b	6.24b	7.05b
Carina	3.44a	6.68a	9.25b	0.87a	4.61a	5.51a	5.06a
Kariega	6.97c	8,05b	12.36d	2.66b	8.34b	6.68b	7.51b
SST 86	3.72a	6.04a	7.99a	1.78a	5.28a	4.88a	4.88a
Mean	5.01a	7.24b	10.12b	2.13a	6.52b	5.73a	

Footnote: Means within the columns followed by the same letter are not significantly different according to Fisher's test (P ≤ 0.05) Each value for grain yield is mean of 16 observations.

Interaction treatment effects on grain yield

The photoperiod x temperature interaction was significant due to the fact that under low temperature (15-5^{0}C) conditions the photoperiod affected the yield more than under warmer temperature (see Table 7.2a). The 13:11 hr/15-5 ^{0}C treatment combination resulted in the highest yield compared to the 11:13 hr/20-15 ^{0}C treatment. The significant interaction between photoperiod x cultivar is shown in Table 7.2b.

All four wheat cultivars produced significantly higher grain yield in the 13:11 hr photoperiod treatment than in the 11:13 hr treatment. The interaction between photoperiod x cultivar was due to the increases in grain yield of Carina (48%) and SST 86 (38%) and Inia (27%), while in the case of Kariega the comparative increase was only 13%. Grain yield of Carina was thus much more affected by photoperiod than Kariega. Table 7.2c shows the significant interaction between temperature x cultivar. The cultivars differed significantly in grain yield in the two temperature regimes. At the higher temperature (20-15^o) the yield of Carina was drastically reduced by as much as 90% of that obtained at the lower temperature (15-5^{o}C). The significant interaction between temperature x cultivar was due to the differential decrease in grain yield under the warmer temperature conditions (20-15 ^{0}C). The significant interaction between vernalization x cultivar is shown in Table 7.2d. Kariega and Inia produced higher grain yield following vernalization but Carina and SST 86 were unaffected by vernalization. The interaction between vernalization x cultivar was due to the differential response in grain yield by Inia and Kariega on one hand and Carina and SST 86 on the other hand. The significant interaction between vernalization x temperature within the 11:13 hr and 13:11 hr photoperiod treatments are shown in Table 7.2e. The absence of a vernalization response by Carina (a winter type) was unexpected, and may be due to the relative short period (10 days) of the vernalization treatment.

Vernalized seed in the short cool days (11:13 hr/15-5 ^{0}C treatment) produced significantly higher grain yield (9.5 g per plant) while under short, warm days (13:11 hr/20-15 ^{0}C treatment) much lower yields were obtained (less than 2 g per plant) and was unaffected by vernalization. Under long, cool days (13:11 hr/15-5 ^{0}C) conditions unvernalized seed reacted more strongly out-yielding vernalized seed (12 vs 11 g per plant), but vernalized seed yielded better than unvernalized seed in the warmer temperature regimes (3 vs 9.9 g per plant) (see Table 7.2e). The higher order interaction between photoperiod, temperature and vernalization was statistically significant but due to the complexity of this interaction no further interpretation is attempted.

TABLE 7.2 Significant interaction effects on grain yield per plant (g)

(a) Photoperiod x temperature

Treatment		**15-5°C**	**20-15°C**
Photoperiod	**11:13 hr**	8.34a	1.68a
	13:11 hr	11.89b	2.58b
		P = 0.0001	P = 0.0322
Mean		10.12	2.13
Mean difference		-3.55	-0.90

(b) Photoperiod x cultivar

Treatment	**Inia**	**Carina**	**Kariega**	**SST 86**
Photoperiod				
11:13 hr	5.92a	3.44a	6.97a	3.72a
13:11 hr	8.18b	6.68b	8.05	6.04b
	P = 0.0003	P = 0.0001	P = 0.0701	P = 0.0002
Mean	7.05	5.06	5.06	4.88
Mean difference	-2.26	-3.24	-1.08	-2.32

Footnote: Means within the columns followed by the same letter are not significantly different according to Fisher's test ($P \leq 0.05$). Each value of grain yield is mean of 16 observations.

(c) Temperature x cultivar

Treatment **Temperature**	**Inia**	**Carina**	**Kariega**	**SST 86**
15-5°C	10.88b	9.25b	12.36b	7.99b
20-15°C	3.22a	0.87a	2.66a	1.78a
	P = 0.0001	P = 0.0001	P = 0.0001	P = 0.0001
Mean	7.05	5.06	7.51	4.88
Mean difference	7.66	8.38	9.70	6.21

(d) Vernalization x cultivar

Treatment	Inia	Carina	Kariega	SST 86
Vernalized	7.86b	4.61a	8.34b	5.28a
Unvernalized	6.24a	5.51a	6.68a	4.49a
	P = 0.0077	P = 0.1333	P = 0.0061	P = 0.1853
Mean	7.05	5.06	7.51	4.88
Mean difference	1.62	-0.90	1.66	0.79

Footnote: Means within the columns followed by the same letter are not significantly different according to Fisher's test (P ≤ 0.05). Each value of grain yield is mean of 16 observations.

(e) Vernalization x temperature x photoperiod

Treatment	Photoperiod 11:13 hr Temperature		Photoperiod 13:11 hr Temperature	
	15-5°C	**20-15°C**	**15-5°C**	**20-15°C**
Vernalized	9.57b	1.93a	11.40a	3.18b
Unvernalized	7.11a	1.43a	12.39b	1.98a
	P = 0.0001	P = 0.3907	P = 0.0976	P = 0.0448
Mean	8.34	1.68	11.89	2.58
Mean difference	2.46	0.50	-0.99	1.20

Footnote: Means within the columns followed by the same letter are not significantly different according to Fisher's test (P ≤ 0.05). Each value of grain yield is mean of 16 observations.

Yield components

Grain number

Main treatment effects

Photoperiod significantly affected number of grains, with the 13:11 hr treatment producing on average 173 grains per plant and the 11:13 hr treatment averaging 125 grains per plant (Table 7.3). The temperature treatment 15-5 ^{0}C produced on average 225 grains per plant compared to the 20-15 ^{0}C temperature treatment at 73 grains per plant (Table 7.3). Vernalization increased grain number, with plants from vernalized seed producing on average 159 grains per plant, and those from unvernalized seed averaging 139 grains per plant. Cultivar differences were observed, averaged over all treatments, with Inia and Kariega producing significantly more grains per plant than SST 86 and Carina (Table 7.3).Carina and SST 86 did not differ in grain number in the vernalized or unvernalized condition.

The photoperiod x temperature interaction within vernalized and unvernalized seed treatments were significant (see Table 7.4d). Vernalized plants reacted more strongly to long, cool days (13:11 hr/15-5 ^{0}C) producing significantly larger number of grains (259 per plant). Vernalized plants under short daylength conditions (11:13 hr photoperiod) reacted much less strongly resulting in lower number of grains being obtained in the warmer temperature conditions (20-15 ^{0}C), while under long daylength conditions (photoperiod 13:11 hr) significantly higher number of grains (108 per plant) was obtained. Similarly, unvernalized plants reacted sharply to the photoperiod 13:11 hr treatment producing significantly larger number of grains (261 per plant) under cool temperature conditions (15-5 ^{0}C). In the warmer temperature (20-15 ^{0}C) lower grain numbers were obtained (ranging between 53 and 65 grains per plant) and where unaffected by the two photoperiod treatments. In real terms, the interaction was due to the strong reaction under long, cool days (13:11 hr/15-5 ^{0}C), by both the vernalized and unvernalized plants, producing larger grain numbers (259-261 per plant) compared to the much smaller reaction of vernalized plants in warm temperature, while unvernalized plants were unaffected by photoperiod. In general, vernalized as well as unvernalized plants in the long, cool days (13:11 hr/15-5 ^{0}C) resulted in higher grain numbers than short, warm day conditions (11:13/20-15 ^{0}C).

TABLE 7.3 Effects of photoperiod, temperature, vernalization and cultivar on grain number per plant of four South African wheat cultivars in controlled growth chamber conditions

Treatment		Photoperiod		Temperature		Vernalization		Cultivar Mean grain number per plant
		11:13 hr	13:11 hr	15-5°C	20-15°C	Vern.	Unvern.	
Wheat	**cultivar**							
	Inia	156.2c	197.7d	251.2d	102.6bc	191.9d	162.0bc	176.9b
	Carina	69.1a	151.8c	191.7c	29.2a	103.2a	117.7a	110.5a
	Kariega	163.1c	181.4cd	253.9d	90.6b	195.6d	149.0b	172.3b
	SST 86	112.9b	164.7c	206.1c	71.5b	147.9b	129.7b	138.8a
Mean		125.3a	173.9b	225.7b	73.5a	159.6b	139.6a	

Footnote: Means within the columns followed by the same letter are not significantly different according to Fisher's test ($P \leq 0.05$). Each value of grain yield is mean of 24 observations.

The photoperiod x vernalization x cultivar interaction was significant and is presented in Table 7.4e. Under vernalization Inia, Carina and SST 86 reacted strongly to long daylength (photoperiod 13:11 hr treatment) producing significantly higher grain numbers than in the short daylength conditions (11:13 hr), but Kariega was unaffected by photoperiod. While number of grains of unvernalized Inia was unaffected by photoperiod treatment, Carina, Kariega and SST 86 produced significantly higher grain numbers under long daylength treatment conditions (photoperiod 13:11 hr). The significant interaction was due to differential increases in grain numbers under long daylength (13:11 hr) by vernalized Carina (44%), Inia (30%) and SST 86 (29%) compared to a non-significant increase by Kariega on the one hand, and to a larger increase in number of grains under long daylength by unvernalized Carina, Kariega and SST 86 on the other hand. Inia reaction to long daylength was much less under unvernalized condition. In general, the cultivars responded similarly to long daylength conditions (photoperiod 13:11 hr) except for Kariega under vernalization and Inia in the unvernalized state.

Mean kernel mass

Main treatment effects

Photoperiod significantly affected mean kernel mass, with the 13:11 hr treatment having the largest kernels averaging 37 mg and the 11:13 hr treatment kernels averaging 32 mg (Table 7.5). Temperature of 15-5 ^{0}C resulted in the largest mean kernel mass averaging 44 mg and the 20-15 ^{0}C treatment the smallest kernels averaging 25 mg (Table 7.5).

Interaction treatment effects on grain number

The photoperiod x temperature interaction was significant for grain number (Table 7.4a). Wheat plants exposed to long, cool days (13:11 hr/15-5 ^{0}C treatment) produced the largest number of grains (260 grains per plant) while those under short, warm days (11:13 hr/20-15 ^{0}C) the lowest (60 grains per plant). In real terms differences in grain numbers between the two photoperiods were greater at the lower temperature (15-5 ^{0}C) treatment than at the higher temperature (20-15 ^{0}C) treatment.

The photoperiod x cultivar interaction is shown in Table 7.4b. In general, the cultivars produced significantly higher grain numbers in the 13:11 hr photoperiod than in the 11:13 hr treatment, with the exception of Kariega which was not affected by photoperiod. The interaction was due to the differential reaction of the cultivars to photoperiod. Carina produced a much larger (54%) number of grains in the 13:11 hr photoperiod, while Kariega was unaffected. The longer photoperiod also resulted in increased grain numbers for SST 86 (31%) and Inia (21%).

The vernalization x cultivar interaction was significant for grain number (see Table 7.4c). Inia and Kariega produced significantly higher grain numbers following vernalization, but Carina and SST 86 did not differ in grain number in the vernalized or unvernalized condition.

When plants were grown under cool conditions (15-5°C) the unvernalized plants reacted mush more (stronger) on photoperiod than vernalized plants. Vernalization softened the deleterious effect of short photoperiods. Under warm conditions (20-15°C) the grain number of unvernalized plants were unaffected by photoperiod, but after vernalization long days resulted in much more grains per plant (108 compared to 66). Similarly, unvernalized plants reacted sharply to the photoperiod 13:11 hr treatment producing significantly larger number of grains (261 per plant) under cool temperature conditions (15-5 ^{0}C). In the warmer temperature (20-15 ^{0}C) lower grain numbers were obtained (ranging between 53 and 65 grains per plant) and where unaffected by the two photoperiod treatments . In real terms, the interaction was due to the strong reaction under long, cool days (13:11 hr/15-5 ^{0}C), by both the vernalized and unvernalized plants, producing larger grain numbers (259-261 per plant) compared to the much smaller reaction of vernalized plants in warm temperature, while unvernalized plants were unaffected by photoperiod. In general, vernalized as well as unvernalized plants in the long, cool days (13:11 hr/15-5 ^{0}C) resulted in higher grain numbers than short, warm day conditions (11:13/20-15 ^{0}C).

TABLE 7.4 Significant interaction effects on grain number per plant

(a) Photoperiod x temperature

Treatment		15-5°C	20-15°C
Photoperiod	11:13 hr	190.6a	60.1a
	13:11 hr	260.8b	87.0b
		P = 0.0001	P = 0.0019
Mean		225.7	73.5
Mean difference		-70.2	-26.9

(b) Photoperiod x cultivar

Treatment	Inia	Carina	Kariega	SST 86
Photoperiodd				
11:13 hr	156.2a	69.1a	163.1a	112.9a
13:11 hr	197.7b	151.8b	181.4a	164.7b
	P = 0.0009	P = 0.0001	P = 0.1315	P = 0.0001
Mean	176.9	110.5	172.51	138.8
Mean difference	-41.5	-82.7	-18.3	-51.8

Footnote: Means within the columns followed by the same letter are not significantly different according to Fisher's test (P ≤ 0.05). Each value of grain yield is mean of 16 observations.

(c) Vernalization x cultivar

Treatment	Inia	Carina	Kariega	SST 86
Wheat plants				
Vernalized	191.9b	103.2a	195.6b	147.9a
Unvernalized	162.0a	117.7a	149.0a	129.7a
	P = 0.0156	P = 0.2315	P = 0.0002	P = 0.1323
Mean	176.9	110.5	172.3	138.8
Mean difference	29.9	-14.5	46.6	18.2

(d) Photoperiod x temperature x vernalization

Treatment	Vernalized		Unvernalized	
	Temperature		Temperature	
	15-5°C	20-15°C	15-5°C	20-15°C
Photoperiod				
11:13 hr	204.1a	66.1a	177.1a	53.9a
13:11 hr	259.9b	108.4b	261.8b	65.6a
	P = 0.0001	P = 0.0007	P = 0.0001	P = 0.3281
Mean	232	87.2	219.4	59.7
Mean difference	-55.8	-42.3	-84.7	-11.6

Footnote: Means within the columns followed by the same letter are not significantly different according to Fisher's test ($P \leq 0.05$).

(e) Photoperiod x cultivar x vernalization

Treatment	Vernalized				Unvernalized			
	Inia	**Carina**	**Kariega**	**SST 86**	**Inia**	**Carina**	**Kariega**	**SST 86**
Photoperiod								
11:13 hr	157.2a	73.8a	187.2a	122.3a	155.2a	64.4a	139.0a	103.5a
13:11 hr	226.5b	132.6b	203.9a	173.6b	168.8a	171.1b	159.0b	155.8b
	P=0.0001	P=0.0008	P=0.3314	P=0.0033	P=0.4304	P=0.0001	P=0.0001	P=0.0028
Mean	191.8	103.2	195.5	147.9	162.0	117.7	149.0	129.6
Mean difference	-69.3	-58.8	-16.7	-51.3	-13.6	-106.7	-20.0	-52.3

Footnote: Means within the columns followed by the same letter are not significantly different according to Fisher's test ($P \leq 0.05$). Each value is a mean of 16 observations.

The photoperiod x vernalization x cultivar interaction was significant and is presented in Table 7.4e. Under vernalization Inia, Carina and SST 86 reacted strongly to long daylength (photoperiod 13:11 hr treatment) producing significantly higher grain numbers than in the short daylength conditions (11:13 hr), but Kariega was unaffected by photoperiod. While number of grains of unvernalized Inia was unaffected by photoperiod treatment, Carina, Kariega and SST 86 produced significantly higher grain numbers under long daylength treatment conditions (photoperiod 13:11 hr). The significant interaction was due to differential increases in grain numbers under long daylength (13:11 hr) by vernalized Carina (44%), Inia (30%) and SST 86 (29%) compared to a non-significant increase by Kariega on the one hand, and to a larger increase in number of grains under long daylength by unvernalized Carina, Kariega and SST 86 on the other hand. Inia reaction to long daylength was much less under unvernalized condition. In general, the cultivars responded similarly to long daylength conditions (photoperiod 13:11 hr) except for Kariega under vernalization and Inia in the unvernalized state.

Mean kernel mass

Main treatment effects

Photoperiod significantly affected mean kernel mass, with the 13:11 hr treatment having the largest kernels averaging 37 mg and the 11:13 hr treatment kernels averaging 32 mg (Table 7.5). Temperature of 15-5 ^{0}C resulted in the largest mean kernel mass averaging 44 mg and the 20-15 ^{0}C treatment the smallest kernels averaging 25 mg (Table 7.5). Vernalization significantly increased mean kernel mass, with kernels from vernalized plants averaging 35 mg, and those from unvernalized plants averaging 34 mg (Table 7.5). Cultivar mean kernel mass, averaged over all treatments, differed significantly with Inia and Kariega mean kernel size averaging 38 mg, while Carina and SST 86 mean kernel size averaged 31 mg. In general, long photoperiod treatments resulted in better grain-filling producing larger kernels irrespective of whether the plants received vernalization treatment or not.

Interaction treatment effects on mean kernel mass

The photoperiod x temperature interaction was significant (see Table 7.6a). At low temperatures (15-5 ^{0}C treatment) photoperiod treatment did not significantly affect mean kernel mass which averaged 44 mg, but at the high temperature (20-15 ^{0}C) kernel mass increased significantly with increasing photoperiod. The 11:13 hr/20-15 ^{0}C treatment combination resulted in the lowest mean kernel mass averaging 20 mg. The significant interaction was due to the difference in mean kernel mass between the two photoperiods in the warmer temperature conditions (20-15 ^{0}C).

Photoperiod x vernalization interaction was significant as shown in Table 7.6b. Vernalized wheat plants produced significantly larger kernels (36 mg) under long day length (13:11 hr photoperiod) conditions than was produced under short daylength (11:13 hr photoperiod). On the other hand unvernalized plants under short daylength (11:13 hr photoperiod) produced much smaller grains (30 mg). The interaction was due to the larger increase in mean kernel mass (19%) in the unvernalized wheat plants compared to a kernel mass increase with vernalized wheat plants.

The photoperiod x cultivar interaction was significant and data is presented in Table 7.6c. The photoperiod 13:11 hr treatment increased significantly mean kernel mass of Carina and SST 86 but not that of Inia and Kariega. The four wheat cultivars produced significantly larger kernels in the 13:11 hr photoperiod treatment than in the 11:13 hr photoperiod. The interaction was due to the large increase in mean kernel mass by Carina (44%), while for Inia and Kariega the increase in mean kernel mass was comparatively small, ranging from 3.2 to 5.8% and was not significant.

TABLE 7.5 Effects of photoperiod, temperature, vernalization and cultivar on mean kernel mass (mg) of four South African wheat cultivars in controlled growth chamber conditions

Treatment	Photoperiod		Temperature		Vernalization		Mean kernel mass (mg)
	11:13 hr mg	13:11 hr mg	15-5°C	20-15°C	Vern.	Unvern.	
Wheat cultivar							
Inia	37.1d	39.2d	46.1e	30.2c	38.7b	37.6b	38.1b
Carina	24.1a	37.8d	46.4e	15.5a	31.5a	30.4a	31.0a
Kariega	37.4c	38.6d	46.2e	29.8c	38.2b	37.7b	38.0b
SST 86	29.8b	32.9c	38.1d	24.6b	32.6a	30.4a	31.3a
Mean	32.1a	37.1b	44.2b	25.0a	35.3b	34.0a	

Footnote: Means within the columns followed by the same letter are not significantly different according to Fisher's test ($P \leq 0.05$). Each value is a mean of 24 observations; vern., vernalized and unvern., unvernalized.

TABLE 7.6 Significant interaction effects on mean kernel mass (mg)

(a) Photoperiod x temperature

Treatment		**15-5°C**	**20-15°C**
Photoperiod	**11:13 hr**	44.1a	20.2a
	13:11 hr	44.4a	29.9b
		P = 0.7975	P =0.0001
Mean		44.3	25.1
Mean difference		-0.3	-9.7

Footnote: Means within the columns followed by the same letter are not significantly different according to Fisher's test (P ≤ 0.05).

(b) Photoperiod x vernalization

Treatment		**Wheat grain**	
		Vernalized	**Unvernalized**
Photoperiod	**11:13 hr**	33.9a	30.3a
	13:11 hr	36.5b	37.7b
		P = 0.0067	P =0.0001
Mean		35.2	34.0
Mean difference		-2.6	-7.4

Footnote: Means within the columns followed by the same letter are not significantly different according to Fisher’s test (P ≤ 0.05).

(c) Photoperiod x cultivar

Treatment	**Inia**	**Carina**	**Kariega**	**SST 86**
Photoperiod				
11:13 hr	37.0a	24.1a	37.4a	29.8a
13:11 hr	39.2a	37.8b	38.6a	32.9b
	P =0.1118	P =0.0001	P =0.3722	P =0.0239
Mean	38.1	31.0	38.0	31.3
Mean difference	-2.2	-13.7	-1.2	-3.1

Footnote: Means within the columns followed by the same letter are not significantly different according to Fisher’s test (P ≤ 0.05).

(d) Temperature x cultivar

Treatment	Inia	Carina	Kariega	SST 86
Temperature				
15-5°C	46.1b	46.5b	46.2b	38.1b
20-15°C	30.2a	15.5a	29.8a	24.6a
	P= 0.0001	P= 0.0001	P= 0.0001	P= 0.0001
Mean	38.2	31.0	38.0	31.4
Mean difference	15.9	30.9	16.4	13.5

Footnote: Means within the columns followed by the same letter are not significantly different according to Fisher's test ($P \leq 0.05$).

(e) Photoperiod x cultivar x vernalization

Treatment	Vernalized				Unvernalized			
Photoperiod	Inia	Carina	Kariega	SST 86	Inia	Carina	Kariega	SST 86
11:13 hr	157.2a	73.8a	187.2a	122.3a	155.2a	64.4a	139.0a	103.5a
13:11 hr	226.5b	132.6b	203.9a	173.6b	168.8a	171.1b	159.0b	155.8b
	P=0.0001	P=0.0008	P=0.3314	P=0.0033	P=0.4304	P=0.0001	P=0.0001	P=0.0028
Mean	191.8	103.2	195.5	147.9	162.0	117.7	149.0	129.6
Mean difference	-69.3	-58.8	-16.7	-51.3	-13.6	-106.7	-20.0	-52.3

Footnote: Means within the columns followed by the same letter are not significantly different according to Fisher's test ($P \leq 0.05$). Each value is a mean of 16 observations.

The significant interaction between temperature x cultivar is shown in Table 7.6d, showing significant lower mean kernel mass of all the cultivars under warmer temperature conditions (20-15 ^{0}C). In real terms, the interaction was due to the larger decrease in mean kernel mass of Carina (66%) compared to small but significant decreases for Inia (34%), Kariega (35%) and SST 86 (35%).

The photoperiod x temperature x cultivar interaction was significant as shown in Table 7.6e. Within the 15-5 ^{0}C temperature treatment the cultivars, except Carina, did not differ significantly in mean kernel mass under the two photoperiods (13:11 hr and 11:13 hr treatments). Within the 20-15 ^{0}C temperature treatment Inia and Kariega did not differ in mean kernel mass in both photoperiod conditions. Carina did not produce any grains in the short, warm days (11:13 hr/20-15 ^{0}C treatment), but in the long, warm days (13:11 hr/20-15 ^{0}C treatment) its kernels averaged 31 mg. The sensitivity of Carina to warmer treatment conditions was indicated by its inability to produce any grains under short, warm days (11:13 hr/20-15 ^{0}C) compared to other cultivars. In real terms, the interaction was due to the inability of Carina to produce any grains under conditions of short, warm days while the other cultivars reacted more or less similarly across the range of photoperiod and temperature treatments. The reaction of Carina to the photoperiod and temperature treatments may have been affected by the length of the vernalization treatment period.

Grain protein content

Main treatment effects

Photoperiod significantly affected grain protein content with the 13:11 hr treatment averaging 19.0% and the 11:13 hr treatment averaging 13.9% (Table 7.7). Temperature differences did not result in significant differences in grain protein content, neither had vernalization any effect. The cultivars differed in grain protein content with Inia at 19% significantly higher than Carina (14.5%) and Kariega (15.9%) (see Table 7.7). The cultivar Carina produced no yield under short, warm days (11:13 hr/20-15 ^{0}C treatment) and hence, yield averaged over other treatments (see Table 7.1, 7.7, 7.8a and 7.8b).

TABLE 7.7 Effects of photoperiod, temperature, vernalization and cultivar on grain protein content (%) of four South African wheat cultivars in controlled chambers

Treatment	Photoperiod		Temperature		Vernalization		Cultivar
	11:13 hr	13:11 hr	15-5 ^{o}C	20-15 ^{o}C	Vern.	Unvern.	Mean grain protein content (%)
Wheat cultivar							
Inia	16.1b	22.0c	20.6ab	17.5ab	16.7a	16.7a	19.0b
Carina	8.1a	20.8c	16.5ab	12.5a	14.6a	14.6a	14.5a
Kariega	15.7b	16.3b	15.3a	16.7ab	16.1ab	16.1ab	15.9a
SST 86	15.9a	16.8a	15.5a	17.2ab	16.8ab	16.8ab	16.4ab
Mean	13.9a	19.0b	16.9a	15.9a	16.9a	16.0a	

Footnote: Means within the columns followed by the same letter are not significantly different according to Fisher's test ($P \leq 0.05$). Each value is am mean of 8 observations; vern., vernalized and unvern., unvernalized.

Interaction treatment effects on grain protein content

The photoperiod x cultivar interaction was significant (see Table 7.8a). The grain protein content of Kariega and SST 86 was unaffected by photoperiod, but in the case of Inia long daylength (13:11 hr photoperiod treatment) resulted in almost 6 percentage point increase in grain protein content. No comparison is made with respect to grain protein content of Carina because it produced no yields under conditions of short, warm days (11:13 hr/20-15 ^{0}C treatment). The significant interaction was due to significant increase in grain protein content of Inia between the two photoperiod treatments. The photoperiod x temperature x cultivar interaction was significant and is presented in Table 7.8b. Within the 11:13 hr photoperiod treatment Inia, Kariega and SST 86 did not significantly differ in grain protein under the two temperatures (15-5 ^{0}C or 20-15 ^{0}C treatment). Comparison is not made between cool (15-5 ^{0}C temperature) and warm (20-15 ^{0}C temperature) treatment conditions because Carina produced no yield under short, warm days (11:13 hr/20-15 ^{0}C treatment). Within the 13:11 hr photoperiod treatment grain protein content of Kariega and SST 86 was unaffected by temperature, but in the case of Inia warmer temperature (20-15 ^{0}C treatment) significantly decreased grain protein content by 31% while that of Carina increased in the 20-15 ^{0}C temperature treatment by approximately 32%. The significant interaction was due to equal but opposite strong reactions to temperature treatments by Inia and Carina within the 13:11 hr photoperiod treatment condition. Because of the complexity of the higher order interaction photoperiod x temperature x cultivar no further explanation is attempted.

The two-way interactions photoperiod x vernalization, photoperiod x temperature, vernalization x temperature, vernalization x cultivars, temperature x cultivar, three-way interactions photoperiod x vernalization x temperature, vernalization x temperature x cultivar and the four-way higher order interaction photoperiod x vernalization x temperature x cultivar were non-significant.

TABLE 7.8 Significant interaction effects on grain protein content (%)

(a) **Photoperiod x cultivar**

Treatment	*Inia*	**Carina**	**Kariega**	**SST 86**
Photoperiod				
11:13 hr	16.1a	8.1a	15.7a	15.9a
13:11 hr	22.0b	20.9b	16.3a	16.8a
	P= 0.0229	P= 0.0001	P= 0.8068	P= 0.7101
Mean	19.0	14.5	15.9	16.4
Mean difference	-5.9	-12.8	-0.6	-0.9

Footnote: Means within the columns followed by the same letter are not significantly different according to Fisher's test ($P \leq 0.05$).

(b) **Temperature x cultivar x photoperiod**

Treatment	**Photoperiod 11:13 hr**				**Photoperiod 13:11 hr**			
	Inia	**Carina**	**Kariega**	**SST 86**	**Inia**	**Carina**	**Kariega**	*SST 86*
Temperature								
15-5°C	15.1a	16.1b	14.6a	15.8a	26.1b	16.9a	15.9a	15.2a
20–15°C	17.1a	0.0a	16.7a	15.9a	17.9a	24.9b	16.7a	18.4a
	P=0.5772	P=0.0001	P=0.5647	P=0.9742	P=0.0252	P=0.0298	P=0.8248	P=0.3699
Mean	16.1	8.1	15.7	15.8	22.0	20.9	16.3	16.8
Mean difference	-2.0	16.1	-2.1	-0.1	8.2	-8.0	-0.8	-3.2

Footnote: Means within the columns followed by the same letter are not significantly different according to Fisher's test ($P \leq 0.05$). Each value is a mean of 16 observations.

7.5 DISCUSSION

Wheat (*Triticum aestivum* L.) is a widely adapted species used as either a spring or winter crop. Temperature and photoperiod have profound effects on grain yield and quality of wheat, controlling the development rate through a multitude of metabolic processes. Grain development can be affected by temperature, photoperiod and vernalization depending on the sensitivity of the particular wheat genotype. The main objective of this trial was to determine the photoperiod, temperature and vernalization effects on grain yield, yield components and grain protein content of four South African wheat cultivars. Understanding the photoperiod, temperature and vernalization response in wheat is important in the prediction of performance and in the development of suitable cultivars for specific growing regions (Nel & Small, 1973; Hammes & Marshall, 1980; Human *et al*., 1981).

Our data indicated that under favourable water and nutrient conditions, higher grain yield, grain number, mean kernel mass and grain protein content was realized in the 13:11 hr/15-5 ^{0}C/vernalization treatments conditions. These plant variables were significantly increased under conditions of long daylength, cool temperatures and vernalization. Grain yields were highest at low temperatures and associated with a longer period of grain growth, while higher temperatures resulted in lower grain yields (Sofield, Evans & Wardlaw, 1974). Similar results for various temperatures imposed during grain-filling have been reported (Thorn, Ford & Watson, 1968; Spiertz, 1977). Plants grown under long daylength and low temperature (13:11 hr/15-5 ^{0}C treatment) produced higher grain yields and grain protein content than those exposed to short daylengths and low temperature conditions (11:13 hr/15-5 ^{0}C treatment) (Tables 7.1 and 7.7) It has been shown in the field that high temperatures during grain-filling period can limit grain yield and higher grain quality (McDonald, Sutton & Ellison, 1983; Sofield, Evans, Cook & Wardlaw, 1977). Experiments under controlled environmental conditions have shown that high temperatures can reduce yield because of individual kernel weights are lower (Koldeup, 1970; Sofield, Evans, Cook & Wardlaw, 1977). Grain quality may be reduced or enhanced by high temperature during grain development depending on cultivar and growth environmental conditions (Finney & Freyer, 1985). For example, it was reported that higher temperatures increased grain protein content levels in the cultivar Schirokko (Schipper, Jahn-Deesbach & Weipert, 1986).

Our data indicate differences in grain yield was associated with increased grain numbers under long daylength and low temperature conditions. The results thus agree with published information that grain number of spring wheat was increased by cool temperature and long photoperiod conditions (Nel & Small, 1973; Fischer & HilleRisLambers, 1978). Plants grown under long daylengths and cool day conditions accumulate large amounts of assimilates from current photosynthesis which is made available to the grains. Our results suggest limited and varied response to vernalization treatments depending on wheat cultivar. Inia, Kariega and SST 86 were less affected by vernalization than Carina. Several authors have reported that expression of vernalization response in spring wheat is influenced by the duration of cold treatment and temperature conditions, while potential yield may not be realised because of unfulfilled vernalization requirements (Evans, Wardlaw & Fischer, 1975; Jedel, Evans & Scarth, 1986; Pinthus, 1985; Wang, Ward, Ritchie, Fischer & Schulthess, 1995). The relationship between grain yield, components of yield, grain protein content and bread-making quality characteristics of wheat as affected with varying soil fertility situations were discussed in Metho, Hammes, De Beer & Groeneveld (1997) and Metho, Hammes & Beyers (1998), respectively. Our results accentuate the importance of quantifying the effects of photoperiod, temperature and vernalization responses of wheat cultivars for breeding and selection for adaptation and improved performance under field conditions. Photoperiod, temperature and vernalization significantly affected grain yield, grain number and mean kernel mass but grain protein content was unaffected by vernalization. The significant interactions between cultivar and the treatments (photoperiod, temperature and vernalization) observed for grain yield, grain number, mean kernel mass and grain protein content indicated strong but different reactions to wheat environmental growth conditions encountered and the effects on grain yield and quality. Vernalized wheat plants, as with Inia and Kariega, reacted more strongly producing higher grain yields, larger number of grains but mean kernel mass and grain protein content varied with temperature and photoperiod, respectively.

In summary, differential responses between cultivars as was with Inia and Kariega on the one hand and SST 86 and Carina on the other hand, indicated potential differences in yield and quality characteristics important in breeding and selection for wheat adaptation and improved yield performance in field conditions. Grain number and protein content were found to be more sensitive to photoperiod, temperature and vernalization treatment effects than mean kernel mass. An index could be constructed to identify cropping regions where grain yield and grain quality is likely to be modified by photoperiod, temperature and vernalization.

7.6 CONCLUSIONS

The interactive effects between photoperiod, temperature and vernalization with four modern South African wheat cultivars were quantified. The significant interactions observed for grain yield, grain number, mean kernel mass and grain protein content indicated differences between the cultivars and their potential abilities to produce yield and quality in response to mainly temperature and photoperiod conditions.

The low temperature regimes (15-5 ^{0}C) and long photoperiod (13:11 hr) treatments resulted in the highest grain yield, number of grains, largest mean kernel size and grain protein content. Under the controlled growth chamber conditions, grain number and grain protein content were found to be more sensitive to photoperiod, temperature and vernalization treatment effects than mean kernel mass.

7.7 REFERENCES

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CHAPTER 8

GENERAL DISCUSSION

This investigation demonstrated that wheat cultivars differ in grain yield, components of yield, grain nitrogen content, grain protein yield, grain protein content, flour yield, loaf volume and in bread-making quality characteristics as a result of varying soil fertility situations. The four wheat cultivars tested generally reacted similarly across the range of soil nutrient regimes. However, significant interactions between cultivar and soil fertility were observed for grain yield, number of grains, mean kernel mass, aboveground biomass, grain protein yield, grain protein content, flour yield and mixograph water absorption, showing differential cultivar reaction.

The effects of long-term NK, NP, PK, NPK and NPK with manure application on yield, yield components and grain quality characteristics were quantified. The hypothesis that wheat cultivars differ in their ability to produce yield and quality under varying or limited soil fertility situations was proven. The hypothesis that tillers affect grain protein content to a greater degree than their contribution to grain yield was disproved. The data indicated that grain protein content of main stems and tillers, as well as grains in different floret positions in the spikelet, did not differ significantly. Fertilization, particularly of the macro-nutrients nitrogen, phosphorus and potassium, is a major input in wheat production, affecting yield and quality (Fischer, 1989; FAO, 1992; Bacon, 1995). Exploiting differences in nutrient utilization efficiency is a strategy on which to focus in the future (Arnon, 1974; Clarkson & Hannon, 1980; Fischer, O'Brien & Quail, 1989). Wheat cultivars with the potential to utilize limited soil nutrients may be important in South Africa and other areas with relatively infertile soils. For example, the ability of Kariega to produce better than the other three cultivars in the K limiting soil fertility situation deserves further investigation. This may be due to Kariega being able to obtain potassium more efficiently from the soil or to lower requirements at the functional sites. This observation may serve as a motivation for deliberate selection of wheat cultivars efficient in nutrient utilization for sustained productivity.

Several authors have reported differential responses for various nutrients in maize, rice, rye, oats and barley (Roberts, Weaver & Phelps, 1972; Wilkes & Scarisbrick, 1974; Mullins & Coffey, 1975; Haag, Adams & Wiersman, 1978). Rice cultivars with differential response to N, P and K have been reported by Fageria, Wright & Baligar (1988) and Fageria (1989). Rye is reported to be more nutrient efficient than other cereals (Nuttonson, 1958; Graham, 1984). Different responses of tomatoes and maize genotypes to N and K are inherited (Clark, 1982). Selection of plants with improved P utilization may be due to plants with root systems capable of intercepting more soil phosphorus, producing large quantities of dry matter and having low metabolic P requirements (Goodwin & Wilson, 1976; Gabelman & Gerloff, 1982; Fageria, 1989). Heritabilty estimates for P or K nutrient utilization efficiency are high but vary with each crop species (Epstein, 1972; Cooke, 1987; Gabelman & Gerloff, 1982). Data on genetics of nutrient utilization variation are still scarce, but evidence exists of single-gene control of micro-nutrient efficiency factors (Graham, 1984). Breeding for nutritional efficiencies is justified in the context of reducing the cost of fertilizer application and environmental pollution (Loneragan, Snowball & Robson, 1976; Graham, 1984). In wheat and rice efficiency of translocation of N from vegetative to reproductive parts during maturation have been responsible for a higher harvest index (Fischer, 1981; Graham, 1984). Identifying wheat genotypes or cultivars, which are efficient in K utilization and uptake may increase yield and quality. This study has indicated that wheat cultivars differ in their utilization of P and K. These differences point to the strategic importance in breeding and selection for wheat genotypes efficient in nutrient utilization.

Data presented in this thesis indicated that the magnitude of compensation between yield components was relatively small. For example, a decrease in number of spikes per m^2 was not adequately compensated for by either grains per spike or kernel mass. Each yield component varied comparatively independently of the others, in agreement with results reported by other researchers (Willey & Holliday, 1971; Gallagher & Biscoe, 1978; Gales, 1983; Hay & Walker, 1989). While no single yield component was predominant in determining yield, number of grains per unit area (a composite component) was highly correlated ($r^2 = 0.95$) with grain yield. Evans (1989) argued that components of yield are inter-dependent to a greater or lesser degree, and that greater number of spikes per unit area is counteracted by a smaller number of grains per spike. The polygon representation of yield and some yield component data (Figure 8.1) shows that the higher grain yield of the cultivar Carina was associated with high number of ears per unit area, spikelets per ear, grains per ear, aboveground biomass production and duration of grain-filling period as indicated by time between anthesis and maturity. The lower yield of SST 86 was due to the low number of ears, low number of spikelets, low grain number and low biomass yield.

In general, results indicated that differences among cultivars in grain yield (Chapter 2), grain protein content and bread-making quality (Chapter 5) occurred mainly in plots low in N, P or K. Significant cultivar x soil fertility interactions were observed for grain yield and some components of yield, biomass and harvest index showing differential cultivar reaction. These results show that in breeding, selection and evaluation the soil fertility conditions should be borne in mind.

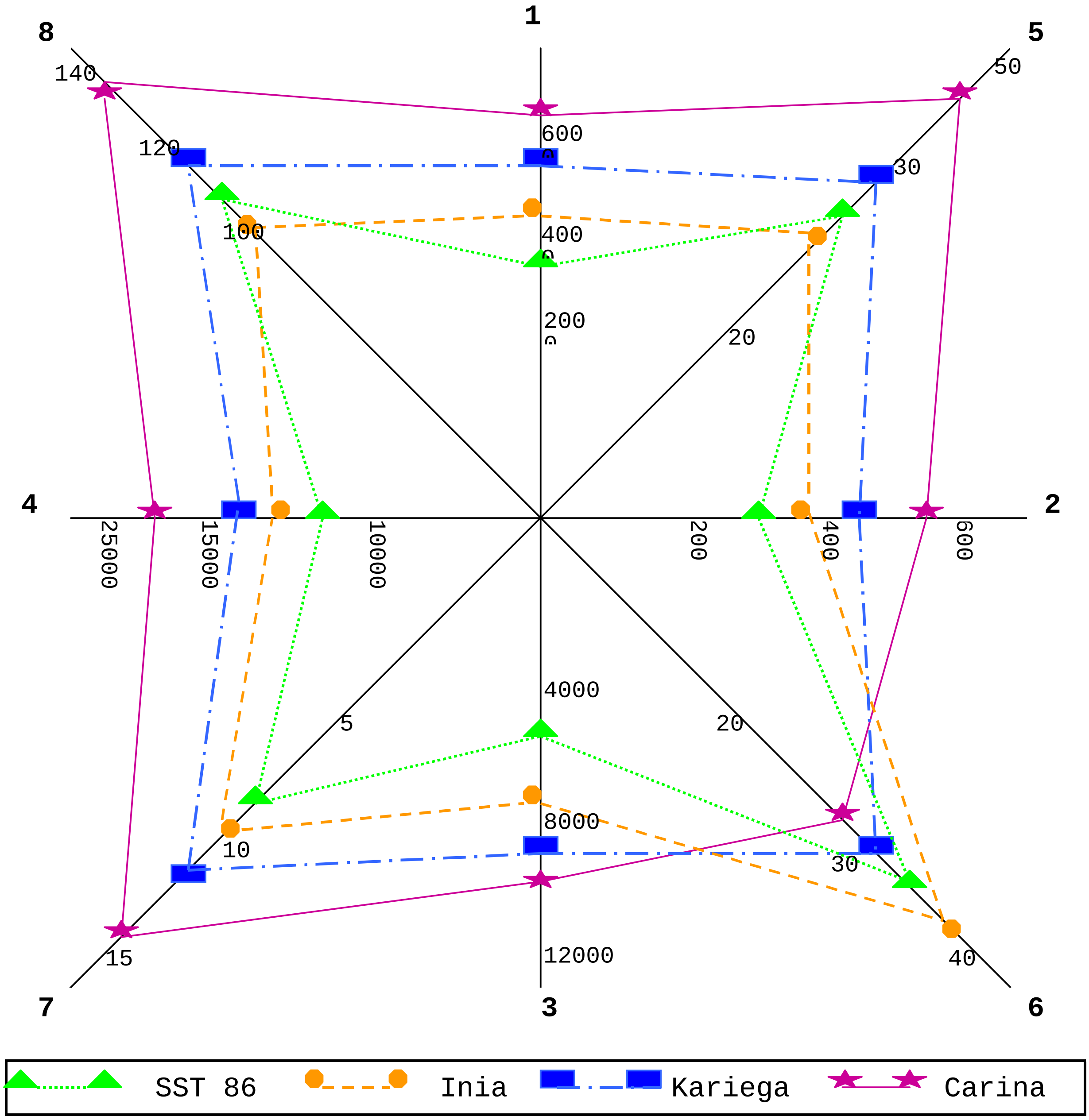

FIGURE 8.1 A polygon representation of average yield and some components of yield of four South African wheat cultivars under six soil fertility situations and date of anthesis (1. Grain yield (kg ha^{-1}); 2. Number of ears (m^{-2}); 3. Number of spikelets (m^{-2}); 4. Grain number (m^{-2}); 5. Grains per ear; 6. Mean grain weight (mg); 7. Biological yield (t ha^{-1}) and 8. Days to 50% anthesis)

The cultivars studied differed in aboveground biomass, harvest index and in ear:vegetative dry-mass ratio with varying soil fertility situations (Chapters 2 and 6). Yield increases have been attributed to genotypic improvements of dry-mass distribution, ear growth rates and phenological developmental pattern from studies comparing old and modern wheat and barley varieties (Austin, Bingham, Blackwell, Evans, Ford, Morgan & Taylor, 1980; Hucl & Baker, 1987; Loss, Kirby, Siddique & Perry, 1989; Perry & D'Antuono, 1995; Siddique, Kirby & Perry, 1995). My data indicated cultivar differences in dry-matter allocation to the ear, and that ear dry weight was positively correlated ($r^2 = 0.65$) to cultivar grain yield. Other studies have shown that increases in potential grain yield have resulted from improvement of the harvest index (Donald & Hamblin, 1976; Austin *et al*., 1980; Blum, 1989). My study extended the concept of harvest index to the individual shoots of a wheat plant. The data indicated that individual wheat ears differ in source-sink potential and partitioning of assimilates to the grain. This may be important in the identification of cultivars efficient in nutrient utilization and improved grain yield.

Few studies have been specifically focused on individual kernel mass and grain protein content by relative floret positions in the spikelet (Briggs, 1991; Gan & Stobbe, 1995). Data obtained during this study is rarely available because data collection is tedious. Nevertheless such information is valuable in crop yield modelling, and may have future benefits in management strategies for maximum yield and quality. Bulman & Smith (1993) reported on the stable nature of main stem ear yield components, and on the relatively small contribution of tillers to grain yield of spring barley. Gan & Stobbe (1995) reported that main stem grain yield was relatively uniform, but tiller yield was highly variable in spring wheat. Briggs (1991) reported that approximately 50% of a plant's productivity in total grains and kernel biomass was produced by the first spike (MS) and 80-90% by the first two spikes (MS and T_1). Our data indicated that main stems (MS) contributed 69%, first tillers (T_1) 25%, second tillers (T_2) 4% and the remaining tillers 2% of the mean yield per unit area, depending on cultivar and growing situation. On average, main stems accounted for 52% of the total fertile ear number per unit area, first tillers 30% and the second tillers 14%, and lower order tillers 4%.

Increasing soil fertility status increased number of main stems, first tillers and second tillers, grain number and hence grain yield and grain protein content. The relative kernel size and grain protein content in the spikelet was not affected by varying fertility. Variability in soil fertility and type are known to have a greater impact on crop yield and quality than other production factors (Carr, Jacobsen, Carlson & Nielsen, 1992).

The four South African wheat cultivars varied significantly in grain quality characteristics. A correlation analysis showed that grain protein content accounted for 65% of the variation in bread-making potential. Positive correlations between grain protein content and loaf volume have been reported (Payne, Holt, Jackson & Law, 1984; Blechl & Anderson, 1998).

Evidence from this study shows that grain protein yield, grain protein content and loaf volume increased with increasing soil fertility and was affected by both wheat cultivar and soil fertility. Several workers have reported increased grain protein content by applying N fertilizer (Dubetz, 1972; Moss, 1973; Laubscher, 1981; Strong, 1986; Carr *et al*., 1992), and breeding and selection for nutrient use efficiency (Noaman, Taylor & McGuire, 1987; Fischer, 1989). In addition, the interface between actual field nutrient status, cultivar productivity and product characteristics as affected by soil fertility situations were demonstrated (Metho, Taylor, Hammes & Randall, 1999; Chapter 5).

The good performance by the cultivar Kariega in the K and P limiting soil fertility situations

(Chapters 3 and 6) and its high loaf volume potential is probably genetic. It is concluded that wheat genotypes and varying soil fertility situations affect bread-making quality characteristics. Further investigation focusing on the variability in loaf volume between cultivars is suggested. For example, information on the relative amounts and quality of the HMW-GS and end-use quality may contribute to the understanding of the variability that exist in loaf volume between wheat genotypes not attributed to grain protein content.

Temperature, photoperiod and vernalization responses of the four wheat cultivars were investigated in the growth chamber experiment. Long, cool days (13:11 hr/15-5 ^{0}C treatment) produced higher grain yield, grain number, larger mean kernel mass and higher grain protein content. In contrast, the short, warm days (11:13 hr/20-15 ^{0}C) resulted in poor performance. Understanding the effects of photoperiod, temperature and vernalization on local wheat cultivars is important for selection, climatic adaptation and yield improvement.

The quantitative information obtained in this study should be of value for crop modelling, especially in wheat yield and quality modelling. In the future, growth models based on the plant's physiological responses will have universal applicability compared to statistical models which are largely site-specific (Sinclair & Amir, 1992; Aggarwal *et al*., 1994). Modelling offers the opportunity to integrate and account for different factors, in addition to acting as a tool for greater understanding of the responses observed experimentally (Sinclair & Amir, 1992; Aggarwal et al., 1994). This is illustrated by the Crop Environmental Resource Synthesis, CERES-Wheat model which forms the basis of the International Benchmark Sites Network for Agrotechnology Transfer, IBSNAT (Uahera, 1985; Ibsnat, 1989).

In my view, and supported by the experience of this research project a wheat plant is able to sense its environment and to adapt its growth and development accordingly, on a continuous basis not yet fully understood. The unravelling or unlocking of this wheat-environment sensor mechanism may be key to accurate modelling of wheat growth, development, yield and grain quality in future.

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RESUMÉ

The experimental material for most of this study was a long-term fertilization and irrigation experiment at the University of Pretoria. The trial provided a good opportunity for studying the performance of different wheat genotypes, over a wide range of soil fertility situations on the same sit. The main objective was to determine the potential ability of wheat genotypes to produce yield and quality under varying soil fertility situations. The interactive effects between photoperiod, temperature and vernalization on grain yield, field components and grain protein content were also quantified in growth chambers.

Deliberate selection of genotypes for nutrient use efficiency is desirable if crop yields are to be maintained. To this regard, I evaluated four South African wheat genotypes for their ability to produce higher yield and desirable grain quality with varying soil nutrient status. The most significant conclusions from this study can be summarized as follows:

1. The interactions observed with respect to grain yield, yield components and grain protein content were largely due to differences between the four wheat cultivars in the K and P limiting soil situations, indicating that wheat cultivars differ in their potential to utilize limited nutrients to produce yield and quality.

2. Grain yield is largely contributed to by main stems and first tillers, and especially the first and second kernels in the spikelet.

3. Late-maturing tillers had the same or higher protein content than the main stem, and in general increased wheat grain protein content.

4. Loaf volume quality was strongly associated with grain protein content level and was significantly reduced in less favourable soil fertility situations.

5. Increasing soil fertility largely increased ear: vegetative dry-mass ratio and hence, harvest index and grain yield potential.

6. Increasing soil fertility increased leaf area index, aboveground biomass accumulation and hence improved grain yield potential.

7. The growth and development pattern was largely influenced by photoperiod-temperatures effects compared to vernalization, indicating that breeding and selection should continue placing emphasis on wheat regional adaptability to specific growing environmental conditions and soil fertility situations.

8. The above results may have implications with regard to wheat breeding and selection objectives, in addition to crop modelling, agronomic applicability and management strategies in different production regions.

APPENDIX

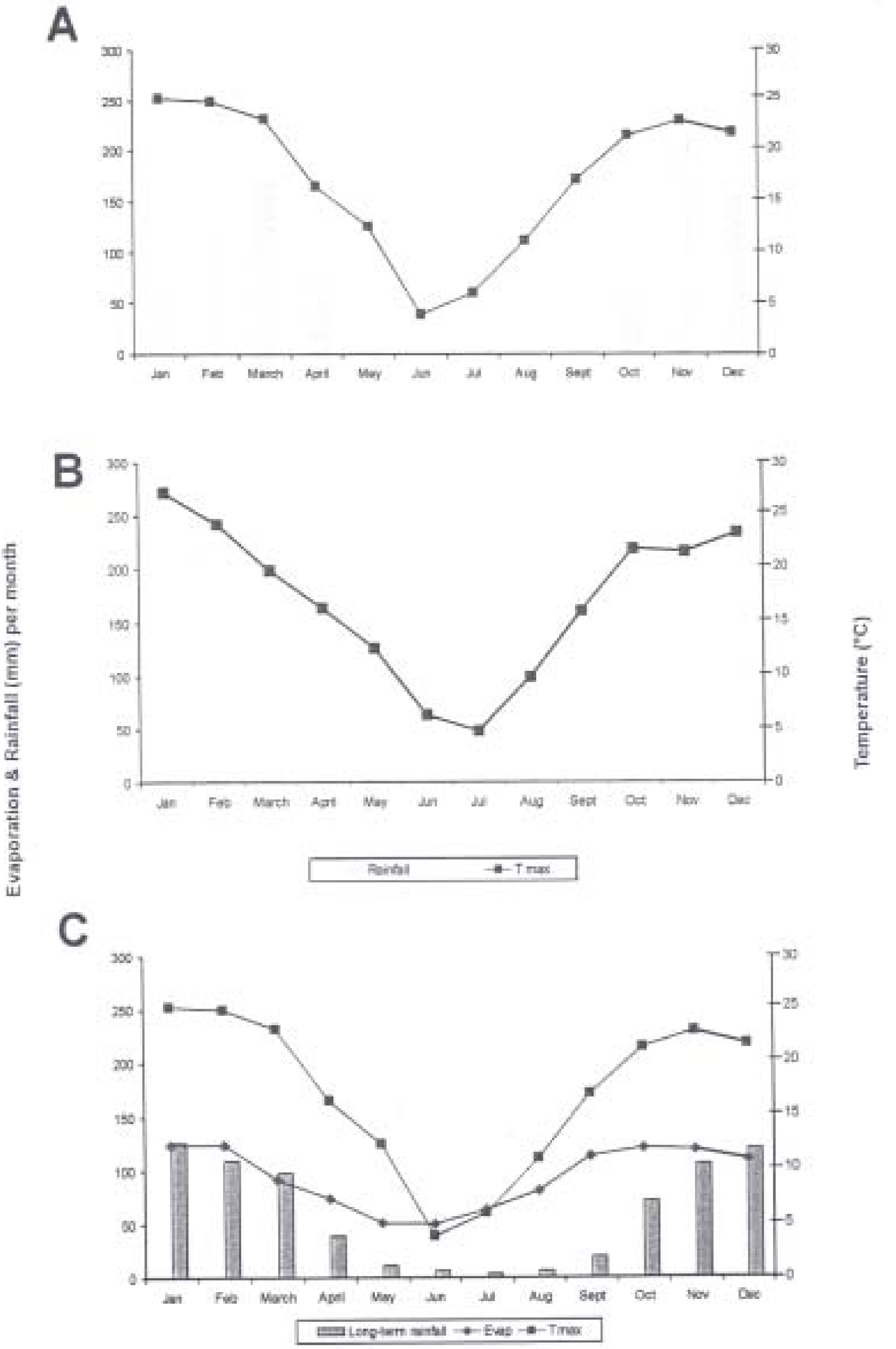

FIGURE 9.A1 Monthly meteorological data for 1995 (A), 1996 (B) and Long-term 1974-1996 (C) for Hatfield Experimental Farm (25°45'S; 28°16'E; altitude 1372 masl) showing mean max temperatures, evaporation and rainfall.

Table 9.A2 Grain yield, spike number, spikelets per spike, grains per spike, grain number, grain mass and grain nitrogen content of three South African spring wheat cultivars at six soil fertility regimes.

Treatment		Grain yield ($kgha^{-1}$)	Spikes (m^{-2})	Spikelets per spike	Grains per spike	Grain number (m^{-2})	1000 grain mass (g)	Grain N content (%)
Cultivar[(1)]	**SST 86**	3373	339	17.1	27.4	10 042	35.2	2.42
	Inia	3742	403	16.9	23.5	10 462	35.9	2.38
	Kariega	4066	426	17.9	27.6	12 827	34.1	2.38
	LSD_T $P_{\leq 0.05}$	466	62.1	1.2	4.1	1 302	1.5	0.08
Fertility	**NPKM**	6163	511	19.6	38.0	19 266	33.9	2.78
	NPK	5590	477	19.2	35.2	16 629	35.1	2.58
	PK	4896	394	18.9	31.8	12 424	39.5	2.16
	NP	3332	475	17.6	24.8	11 903	27.8	2.31
	NK	1300	260	14.7	13.7	3 523	36.6	2.39
	O	1081	219	13.0	13.6	2 918	37.4	2.13
	LSD_T $P_{\leq 0.05}$	1480	168	1.9	11.9	3 880	3.9	0.30
CV %		18.3	21.5	9.7	21.7	16.6	5.8	5.4

Significant at the 0.05 level.

(1) Data exclude the cultivar Carina which had missing values

TABLE 9.A3 Grain yield and components of yield performance of four South African wheat cultivars at three soil fertility regimes

Treatment		Grain yield (kg ha^{-1})	Spikes (m^{-2})	Spikelets per spike	Grains per spike	Grain number (m^{-2})	1000 grain mass (g)	Grain N content (%)
Cultivar	**SST 86**	3903	349	16.9	29.3	11650	36.2	2.47
	Inia	4484	403	16.7	27.6	12342	36.9	2.53
	Kariega	4447	454	18.2	29.9	14821	33.4	2.49
	Carina[1]	6343	508	20.1	42.8	23956	27.4	3.58
	LSD_T $P_{\leq 0.05}$	1031	100	2.0	10.5	3587	2.1	0.98
Fertility	**NPKM**	6801	546	20.2	41.3	23269	31.8	3.00
	NPK	6253	496	19.5	40.2	19838	33.3	2.84
	'O' Control	1330	244	14.2	15.7	3970	35.4	2.46
	LSD_T $P_{\leq 0.05}$	1392	149	1.9	9.2	2474	1.5	0.11
CV %		20.0	22.6	9.4	26.9	17.9	4.9	26.5

Significant at the 0.05 level.

(1) Yield data for Carina was obtained for the treatments NPKM, NPK and 'O' only.

TABLE 9.A4 Effect of cultivar and soil fertility on biomass yield, harvest index and crop height at six soil fertility regimes at maturity

Treatment		Biomass ($t\ ha^{-1}$)	Harvest index	Crop height (mm)
Cultivar	**SST 86**	8.3	0.33	674
	Inia	9.9	0.29	903
	Kariega	11.1	0.32	855
	LSD_T $P \leq 0.05$	1.1	0.03	63.9
Fertility [1]	**NPKM**	15.5	0.37	950
	NPK	13.8	0.36	919
	PK	12.0	0.37	886
	NP	9.1	0.32	736
	NK	4.2	0.26	692
	'O' Control	3.9	0.22	682
	LSD_T $P \leq 0.05$	3.3	0.11	75.6
CV %		16.3	9.9	6.1

Significant at the 0.05 level.
[1] **Fertility data excludes Carina.**

TABLE 9.A5 Biomass yield, harvest index and final crop height of four South African wheat cultivars at three soil fertility regimes

Treatment		Biomass (t ha^{-1})	Harvest index	Crop height (mm)
Cultivar[(1)]	**SST 86**	9.4	0.33	709
	Inia	11.4	0.29	943
	Kariega	12.3	0.32	900
	Carina	15.0	0.36	1018
	LSD_T P $\leq$ 0.05	1.5	0.01	64.0
Fertility	**NPKM**	15.5	0.37	950
	NPK	13.8	0.35	919
	'O' Control	4.3	0.25	729
	LSD_T P $\leq$ 0.05	1.6	0.04	516
CV %		11.1	15.4	5.2

Significant at the 0.05 level
(1) Cultivar data based on treatments NPKM, NPK and '0' only.

TABLE 9.A6 Interaction between cultivar and soil fertility on grain number per ear of first and second tillers (T_1 and T_2) of four South African wheat cultivars

(a) First tiller (T_1)

Treatment		GRAINS PER EAR			
		CULTIVAR			
		SST 86	Inia	Kariega	Carina
Fertility	NPKM	30.8a	17.4a	34.4a	25.3a
	NPK	32.6a	33.3b	28.9a	38.8a
	LSD_T $P \leq 0.05$	14.5			
CV (%)		12.9			

(b) Second tiller (T_2)

Treatment		GRAINS PER EAR			
		CULTIVAR			
		SST 86	Inia	Kariega	Carina
Fertility	NPKM	22.6a	3.4a	17.4a	13.9a
	NPK	14.4a	15.6b	16.4a	18.8a
	LSD_T $P \leq 0.05$	12.9			
CV (%)		22.4			

Significant at the $P \leq 0.05$ level.

TABLE 9.A7 Interaction between cultivar and soil fertility on grain protein content of four South African wheat cultivars with respect to first and second tillers (T_1 and T_2)

(c) First tiller (T_1)

Treatment		GRAIN PROTEIN CONTENT (%)			
		CULTIVAR			
		SST 86	Inia	Kariega	Carina
Fertility	NPKM	15.5a	14.3a	14.5a	14.5a
	NPK	15.0a	15.1a	16.7b	15.4a
	LSD_T $P \leq 0.05$		2.2		
CV (%)			6.9		

(d) Second tiller (T_2)

Treatment		GRAIN PROTEIN CONTENT (%)			
		CULTIVAR			
		SST 86	Inia	Kariega	Carina
Fertility	NPKM	14.1a	14.1a	15.4a	14.6a
	NPK	17.6b	15.1a	16.9b	15.4a
	LSD_T $P \leq 0.05$		1.49		
CV (%)			3.9		

Significant at the $P \leq 0.05$ level.

TABLE 9.A8 Interaction between cultivar and soil fertility on grain protein content by floret position of four South African wheat cultivars

Treatment		GRAIN PROTEIN CONTENT (%)			
		CULTIVAR			
		SST 86	Inia	Kariega	Carina
Fertility	**NPKM**	14.5a	13.7a	12.9a	15.4b
	NPK	13.9a	14.5b	15.7b	14.3a
	LSD_T $P_{\leq 0.05}$			0.69	
CV (%)				5.3	

Significant at the P ≤ 0.05 level.

TABLE 9.A9 Comparison of effect of cultivar and soil fertility on nitrogen harvest index and grain protein content (%) of four South African wheat cultivars between 1995 and 1996.

Treatment		1995[1]		1996[2]	
		NHI	GPC (%)	NHI	GPC (%)
Cultivar					
	SST 86	0.77a	12.0a	0.73a	13.7a
	Inia	0.78a	11.5a	0.85b	13.5a
	Kariega	0.79a	11.6a	0.79a	13.5a
	Carina	0.81b	13.1b		14.4b
Fertility					
	NPKM	0.73a	13.8d		
	NPK	0.78a	13.3d	0.78a	12.5c
	PK	0.83b	9.7a	0.83b	9.4a
	NP	0.76a	10.9b	0.76a	10.0b
	NK	0.75a	11.9c	0.75a	11.4b
	'O' Control	0.84b	10.4b		
Mean		0.78	11.7	0.78	10.8
CV %		5.3	5.7	4.9	6.6

Means within the columns followed by the same letter are not significantly different according to Fischer's test (P ≤ 0.05).
[1] **Fertility data excludes Carina.**
[2] **Cultivar data based on treatments NPK, PK, NP and NK only.**

TABLE 9.A10 Effect of soil fertility status on bread-making quality characteristics of two South African wheat cultivars

Treatment		Loaf volume[2] (cm^3)	Mixograph peak water absorption (%)	Mixograph peak time (min)	Dough characteristics
NPK[3]	Inia	950	63.4	3.4	Normal
	Kariega	1025	63.2	3.6	Normal
	Mean	988c*	63.3b	3.5a	
PK	Inia	880	63.0	3.8	Normal
	Kariega	880	59.4	3.7	Normal
	Mean	880a	61.2a	3.8b	
NP	Inia	920	61.7	3.5	Normal
	Kariega	1040	62.7	3.7	Normal
	Mean	980c	62.2ab	3.6ab	
NK	Inia	890	61.8	4.0	Normal
	Kariega	980	63.4b	3.6	Normal
Mean		935b	62.6b	3.8b	
CV %		1.3	1.5	3.5	

*** Significant at the P ≤ 0.05 level.**