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 $P \leq 0.05$.
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 $P \leq 0.05$.
1 Cultivar data based on fertility treatments NPKM, NPK and Control 'O' only.

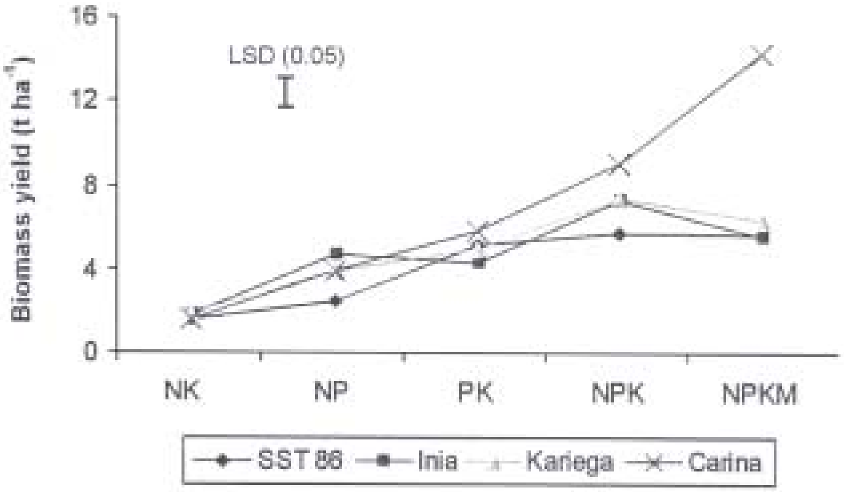

FIGURE 6.1 Interaction between soil fertility and cultivar on biological yield of four South African wheat cultivars at terminal spikelet stage.

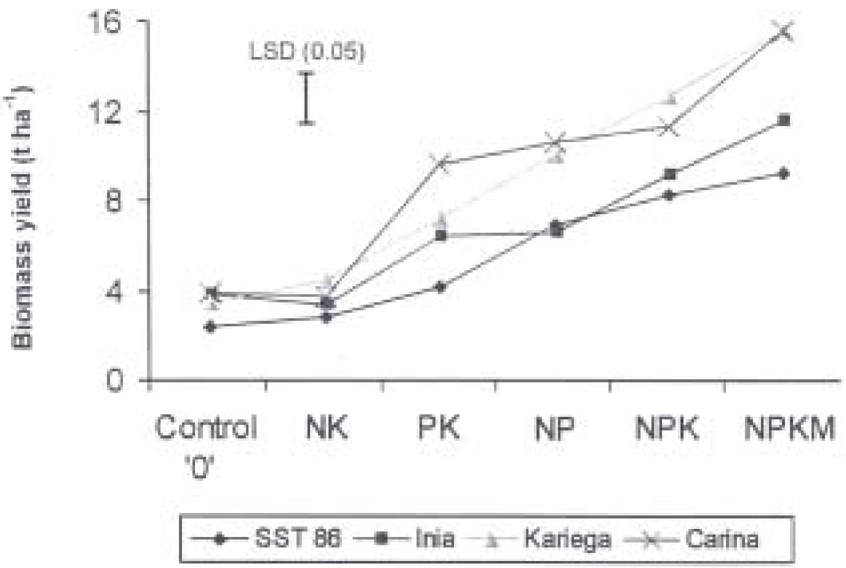

FIGURE 6.2 Interaction between soil fertility and cultivar on biological yield of four South African wheat cultivars at 50% anthesis.

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.

6.7 REFERENCES

AASE, J.K.,1975. Relationship between leaf area and dry matter in barley. *Montana Agric. Exp. J.* 361-327.

AASE, J.K., 1977. Growth, water use and energy balance comparisons between isogenic lines of barley. *Agron. J.* 63, 425-428.

AASE, J.K., 1978. Relationship between leaf area and dry datter in Winter Wheat. Montana *Agric. Exp. Stn. J.* 563-568.

AUSTIN, F.B., BINGHAM, J., BLACKWELL, R.D., EVANS, L.T., FORD, M.A., MORGAN, C.L. & TAYLOR, M., 1980. Genetic improvements in winter wheat yields since 1900 and associated physiological changes. *J. Agric. Sci.* 94, 675-689.

ANNANDALE, J.G., HAMMES, P.S. & NEL, P.C., 1987. Effect of soil fertility on the vegetative growth, yield and water use of wheat *(Triticum aestivum L.). S. Afr. J. Plant Soil.* 1, 96-97.

BISCOE, P.V., SCOTT, R.K. & MONTEITH, J.J., 1975. Barley and its environment. III. Carbon budget of the stand. *J. of A. Ecol.* 12, 269-293.

BISCOE, P.V., 1979. Basic cereal physiology and its application to wheat. In Course Papers: *The yield of cereals,* pp. 7-19. Stoneleigh: National Agricultural Centre, Cereal Unit.

BISCOE, P.V. & WILLINGTON, V.B.A., 1984. Environmental effects on dry matter production. In *The Nitrogen Requirements of Cereals.* Reference book 3851, Ministry of Agriculture, Fisheries and Food, HMSO, pp. 53-65.

BLACK, J.N., 1963. The interrelationship of solar radiation and leaf area in determining the rate of dry matter production of swards of subterranean clover (*Trifolium subterrenean* L.). *Aust. J. Agric. Res.* 14, 20-38.

BLACKMAN, G.E., 1956. Influence of light and temperature on leaf growth. p. 151-167. *In Milthorpe,* F. L. (ed.). The growth of leaves. Butterworths, London.

BRADFORD, K.J. & HSIAO, T.C., 1982. Physiological responses to moderate water stress. In: "Encyclopedia of plant physiology, N.S. Physiological plant ecology II. Water relations and carbon assimilation." Lange *et al*., Eds., Springer-Verlag, berlin/N.Y. pp. 263-324.

BROOKING, I.R. & KIRBY, R.J.M., 1981. Interrelationships between stem and ear development in winter wheat: The effects of Norin 10 dwarfing gene. Gai/Rht2. *J. Agric. Sci. Camb.* 97, 373-381.

COCK, J.H. & YOSHIDA, S., 1973. Photosynthesis, crop growth and respiration of tall and short rice varieties. *Soil Sci. and Plant Nutrition.* 19, 53-59.

FISCHER, R.A. & STOCKMAN, Y.M., 1986. Increased kernel number in Norin 10-derived dwarf wheat: Evaluation of the cause. *Aust. J. Plant Physiol.* 13, 767-787.

GALLAGHER, J.N. & BISCOE, P.V., 1978. A physiological analysis of cereal yield. II. Partitioning of dry matter. *Agric Progress.* 51-70.

INNES, P. & BLACKWELL, R.D., 1983. Some effects of leaf posture on the yield and water economy of winter wheat. *J. Agric. Sci. Camb.* 101, 367-401.

JAIN, H.K. & KULSHRESTHA, V.P., 1976. Dwarfing genes and breeding for yield in bread wheat. *Z. Pflanzenzucht.* 76, 102-112.

MARSHALLS, J.K., 1968. Methods for leaf are measurements of large and small leaf samples. *Photosynthetica (Prague*). 2, 41-47.

McLERAN, J.S., 1981. Field studies on the growth and development of winter wheat. *J. Agric. Sci. Camb.* 97, 685-697.

METHO, L.A., HAMMES, P.S., DE BEER, J.M. & GROENEVELD, H.T., 1997. Interaction between cultivar and soil fertility on grain yield, yield components and grain nitrogen content of wheat. *S. Afr. Plant Soil.* 14, 158-164.

MEYER, W.S. & GREEN, G.C., 1980. Water use by wheat and plant indicators of available soil water. *Agron. J.* 72, 253-257.

MULDOON, J.F., DAYNARD, T.B., VAN DUINEN, B. & TOLLENAAR, M., 1984. Comparison among rates of appearance of leaf tips, collars and leaf area in maize (*Zea mays* L.). *Maydica*. 29, 109-120.

NEL, P.C., BARNARD, R.O., STEYNBERG, R.E., DE BEER, J.M. & GROENEVELD, H.T., 1996. Trends in maize yields in a long-term fertilizer trial. *Field Crops Research.* 3, 225-234.

PERRY, M.W. & D'ANTUONO, M., 1989. Yield improvement and associated characteristics of some Australian spring wheats introduced between 1860 and 1982. *Aust. J. Agric. Res.* 40, 457-472.

ROEBUCK, J., 1981. A re-appraisal of growth regulators. *Winter wheat - Proceedings of the 16th NIAB Crop Conference,* 1980, 47-52. Cambridge: National Institute of Agricultural Botany.

SIDDIQUE, K.H.M, KIRBY, R.J.M & PERRY, M.W., 1989. Ear:stem ratio in old and modern wheat varieties; relationship with improvement in number of grains per ear and yield. *Field Crops Research*. 21, 59-78.

WALKER, S., 1988. Spatial pattern of leaf growth of sorghum as affected by water stress and implications for canopy development. *Ph.D. diss., University of California, Davis*. pp. 134.

WATSON, D.J., 1937. The estimation of leaf area in field crops. *J. Agric. Sci.* 27, 474-483.

WATSON, D.J., THORNE, G.N. & FRENCH, S.A.W., 1963. Analysis of growth and yield of winter and spring wheats. *Ann. Bot.* 27, 1-22.

ZRUST, J.E., PARTYKOVA & NECAS, J., 1974. Relationships of leaf area to leaf weight and length in potato plants. *Photosynthetica (Prague*). 8, 118-124.