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

Publication based on this study:

Metho, L.A., Hammes, P.S., Groeneveld, H.T. & Beyers, E.A., 1999. Effects of photoperiod and temperature on grain yield, grain number, mean kernel mass and grain protein content of vernalized and unvernalized wheat (*Triticum aestivum* L.). *Biotronics.* (Vol 28).

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 $0\,^0C$ to $11\,^0C$ (Gott, 1961; Aherns & Loomis, 1963). It has been reported that the optimum temperature was $11\,^0C$ for spring wheat and $3\,^0C$ 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 $\mu Em^{-2}\,sec^{-1}$, as measured by a Lambda Instruments Model LI 185 quantum meter.

The temperature treatments used were 20/15 ^0C and 15/5 ^0C 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 ^0C 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 ($P \leq 0.05$) 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°) the yield of Carina was drastically reduced by as much as 90% of that obtained at the lower temperature (15-5°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 ≤ 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 ($P \leq 0.05$). 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 ($P \leq 0.05$). 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 ≤ 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 ($P \leq 0.05$).

113

(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 ≤ 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	13:11 hr	15-5°C	20-15°C	Vern.	Unvern.	
	mg	mg					
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 ≤ 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 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).

121

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 ≤ 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 ≤ 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

A A C C, American Association of Cereal Chemists 1986 Method 46-13; Crude protein - micro Kjeldhal Method. *Approved Methods* of AACC (8th Edition, update in use), St. Paul, Minnesota.

AHERNS, J.F. & LOOMIS, W.E., 1963. Floral induction and development in winter wheat. *Crop Sci.* 3, 463-466.

DOWNS, R.J. & HELLMERS, H., 1975. Temperature. Pages 7-30 in *Environment and the Experimental Control of Plant Growth*. Academic Press, New York.

EVANS, L.T., WARDLAW, I.F. & FISCHER, R.A., 1975. Wheat. Pages 101-149 in L.T. EVANS (ed.) *Crop Physiology*. Cambridge University Press, Cambridge.

FINNEY, K.F. & FRYER, H.C., 1958. Effect on loaf volume of high temperatures during the fruiting period of wheat. *Agron. J.* 50, 28-34.

FISCHER, R.A. & HILLERISLAMBERS, D., 1978. Effect of Environment and Cultivar on Source Limitation to Grain Weight in Wheat. *Aust. J. Agric. Res.* 29, 443-458.

FRIEND, D.J.C., FISCHER, J.E. & HELSON, V.A., 1963. The effect of light intensity and temperature on floral initiation and inflorescence development of Marquis wheat. *Can. J. Bot.* 41, 1663-1674.

GOTT, M.B., 1961. Flowering of Australian wheats and its relation to frost injury. *Aust. J. Agric. Res.* 12, 547-565.

HAMMES, P.S. & MARSHALL, R.J., 1980. Effect of photoperiod and temperature on the developmental rate of three cultivars of wheat (*Triticum aestivum* L.). *Field Crops Research*. 3, 121-128.

HOSHIKAWA, K., 1961. Studies on the ripening of wheat. 4. The influence of temperature on endosperm formation. *Proc. Crop Sci.* Japan 30, 228-231.

HUMAN, C.H., NEL, P.C., HAMMES, P.S. & BEYERS, E.A., 1981. 'n Voorgestelde wysiging van die Zadokssleutel ten einde groeipunstadia te kan inkorporeer, na aanleiding van 'n ondersoek met koring. *Crop Production.* Vol. X. 171-175.

JEDEL, P.E., EVANS, L.E. & SCARTH, R., 1986. Vernalization response of a selected group of spring wheat (*Triticum aestivum* L.) cultivars. *Can. J. Plant Sci.* 66, 1-9

JOUBERT, G.D. & LAUBSCHER, E.W., 1974. Bepaling van daglengtevereistes by koring. *Crop Production.* 3, 29-32.

JUNGES, W., 1959. Beeinflussung des Bluhbeginns annueller landwirtschaflicher und gartnerischer Kulturpflanzen durch Jarowisation bei Konstanten Temperaturen Zwischen - 10^0 und + 35 ^{0}C. Z. fur *Pflanzen.* 41, 103-122.

KOLDERUP, F., 1975. Effects of temperature, photoperiod and light quality on protein production in wheat grains. *J. Sci. Food Agric.* 26, 585-592.

LEVY, J. & PETERSON, M.L., 1972. Response of spring wheats to vernalization and photoperiod. *Crop Sci.* 12, 487-490.

McDONALD, G.K., SUTTON, B.G. & ELLSION, F.W., 1983. The effect of time of sowing on the grain yield of irrigated wheat in Namoi Valley, New South Wales. *Aust. Agric. J. Res.* 34, 224-229.

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. J. Plant Soil.* 14, 158-164.

METHO, L.A., HAMMES, P.S. & 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.

MIDMORE, D.J., CARTWRIGHT, P.M. & FISCHER, R.A., 1984. Wheat in tropical environments. II. Crop growth and yield. *Field Crops Research.* 8, 207-227.

MITCHELL, R.A.C., LAWLOR, D.W. & YOUNG, A.T., 1991. Dark respiration of winter wheat crops in relation to temperature and simulated photosynthesis. *Ann. Bot.* 67, 7-16.

NEL, P.C. & SMALL, J.G.C., 1973. Photoperiod and temperature effects on yield of four South African wheat cultivars. *Agroplantae.* 5, 25-32.

NITSCH, J.P., 1972. Phytotrons: past achievements and future needs. In: A.R. Rees, K.E. Cockshull, D.W. Hand and R.G. Hurd (Ed.) Crop Processes in Controlled Environments. Academic Press. London, 33-55.

PINTHUS, M.J., 1985. *Triticum.* In: A.H. Halevy (Ed.). CRC Handbook of Flowering, Vol. IV. CRC Press, Boca Raton, FL, 418-443.

RAWSON, H.M., 1970. Spikelet number, its control and relation to yield per ear in wheat. *Aust. J. Biol. Sci.* 23, 537-546.

SALISBURY, F.B., 1979. Temperature. Pages 75-116. In T.W. Tibbitts and T.T. Kozlowski (eds.) *Controlled Environment Guidelines for Plant Research.* Academic Press, New York.

SAS INSTITUTE, 1989. SAS/STAT user's guide. 5th Edition. SAS Inst., CARY, NC.

SCHIPPER, A., JAHN-DEESBACH, W. & WEIPERT, D., 1986. Untersuchungen zum Klimaeinfluss auf die Weizenqualitat. *Getrude Mehl un Brot.* 40, 99-103.

SIM, J.T.R., 1965. Koringproduksie in Suid - Afrika. *Bull. Dept. L.T.D.* No. 377.

SOFIELD, I., EVANS, L.T. & WARDLAW, I.F., 1974. The effect of temperature and light on grain filling in wheat. In: 'Mechanisms of Regulation of Plant Growth'. *Int. Plant Physiol. Symp.*, N.Z.R. Soc.

SOFIELD, I., EVANS, L.T., COOK, M.G. & WARDLAW, I.F., 1977. Factors influencing the rate of and duration of grain filling in wheat. *Aust. J. Plant Physiol.* 4, 785-797.

SPIERTZ, J.H.J., 1974. Grain growth and distribution of dry matter in the wheat plant as influenced by temperature, light, energy and ear size. *Neth. J. Agric. Sci.* 22, 207-220.

SPIERTZ, J.H.J., 1977. The influence of temperature and light intensity on grain growth in relation to the carbohydrate and nitrgoen economy of the wheat plant. *Neth. J. Agric. Sci.* 25, 182-197.

STEEL, R.G.D. & TORRIE, J.H., 1980. Principles and Procedures of Statistics 2nd ed. McFraw-Hill, New York. 428-471.

THORNE, G.N., FORD, M.A. & WATSON, D.J., (1968). Growth, development and yield of spring wheat in artificial climates. *Ann. Bot.* 32, 425-446.

WALL, P.C. & CARTWRIGHT, P.M., 1974. Effects of photoperiod, temperature and vernalization on the phenology and spikelet numbers of spring wheats. *Ann. Appl. Biol.* 76, 299-309.

WANG, S.Y., WARD, R.W., RITCHIE, J.T., FISCHER, R.A. & SCHULTHESS, U., 1995. Vernalization in wheat. II. Characterization of vernalization response of a diverse et of genotypes. *Field Crops Research 44, 67-72.*.

WARDLAW, I.F., 1970. The early stages of grain development in wheat: response to light and temperature in a single variety. *Aust. J. Biol. Sci.* 23, 765-774.

WARRINGTON, I.J., DUNSTONE, R.L. & GREEN, L.M., 1977. Temperature effects at three development stages on the yield of the wheat ear. *Aust. J. Agric. Res*. 28, 11-27.