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.)

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METHO L. A., HAMMES P. S., GROENEVELD H. T. and BEYERS E. A. *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 **28**, 55–71. Wheat is grown under divergent climatic conditions in South Africa, varying from cool short days to warm long days. 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 unbernalized seed of four wheat cultivars (Inia, Carina, Kariega and SST 86) were grown in growth chambers comprising two photoperiods and two temperature regimes (photoperiod 11 hr/temperature 20–15℃; 13 hr/20–15℃; 11 hr/15–5℃ and 13 hr/15–5℃). Temperature treatments were applied on a 12 hr–12 hr basis. In the 13 hr/15–5℃ treatment the grain yield averaged 11.9 g per plant with a 18.5% grain protein content. In the 11 hr/20–15℃ treatment the yield averaged 1.7 g per plant with a 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 14 to 25% higher, but vernalization did not affect the yield of SST 86 and Carina. The interactions: photoperiod and temperature; photoperiod and cultivar; and photoperiod, temperature and cultivar were significant with respect to grain yield, grain number, mean kernel size and grain protein content. The low temperature (15–5℃) 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 conditions.

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

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INTRODUCTION

When plants are exposed to longer daylengths and/or lower night temperatures, production is often improved through a balance between photosynthesis and respiration (*3, 24, 21*). In South Africa, wheat (*Triticum aestivum* L.) is grown under widely divergent climatic conditions, varying from cool short days to warm long days (*22, 10*). Understanding the reaction of local wheat cultivars to varying photoperiod and temperature conditions, as manifested in the grain yield and grain quality characteristics, can improve regional wheat yield and quality.

Several studies on the effects of photoperiod, temperature and vernalization of wheat have been reported, but few have analyzed the interactive effects on yield and grain protein content (*38, 13, 39, 10*). 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 (*39*). High spikelet numbers at low temperatures are due to a much longer period of spikelet differentiation (*7*). Other writers have reported that at high temperature (30℃) grain repening was accelerated and this resulted in smaller grains at maturity (*9, 20*). 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 (*30*). Similar results for various temperatures imposed during the grain growth stage have been reported (*32*). It has been reported that flower induction of wheat exposed to longer days was hastened causing a reduction in spikelet number (*25, 35, 36*).

In South Africa wheat may be sown in spring, autumn or winter depending on the production area. Most local cultivars, even those grown in the Winter Rainfall Region, are spring wheats (*29*). 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 flowering and may increase the number of spikelets differentiated, and hence yield capacity (*16, 25*). Vernalization temperatures range between 0℃ to 11℃ (*8, 2*). It has been reported that the optimum temperature is 11℃ for spring wheat and 3℃ for winter wheat (*14*).

The main objective of the trial reported 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 in controlled growth environments.

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, of the 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℃ and 15/5℃ 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.

General procedure and plant materials

Certified seed of four spring 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℃ 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 (*23*), 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 a 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. They are 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, Western Cape and in the Eastern Gauteng Province where it is sown at the begining 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 and mean kernel mass were determined on a per plant and per pot basis (plant material was oven dried at 60℃ for 48 hr). Grain nitrogen was measured by the Kjeldhal method (*1*), and grain protein content was estimated as N X 5.7 (*1*).

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 computer program (*27*). 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 (*34*). Due to the missing or unbalanced nature of the data Fisher's test was performed.

RESULTS

The main effects of photoperiod, temperature, vernalization and cultivar on grain yield, grain number, mean kernel mass and prain protein content are shown in Tables 1, 3, 5 and 7. Significant interactions between photoperiod × temperature, photoperiod × cultivar, vernalization × cultivar, photoperiod × temperature × cultivar and photoperiod × vernalization × cultivar for grain yield, grain number, mean kernel mass and grain protein content are shown in Tables 2a–e, 4a–e, 6a–e, and 8a–b. The other treatment interactions were not statistically significant.

(1) 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 1). Temperatures of 15–5℃ resulted in a significantly higher grain yield averaging 10.1 g per plant compared to 2.1 g per plant for the 20–15℃ temperature treatment (Table 1). Vernalization significantly increased grain yield, with plants from vernalized seed yielding 6.5 g per plant, while those from unvernalized seed averaged 5.7 g per plant (Table 1). Cultivar grain yield averaged over all treatments differed significantly with Kariega and Inia

Table 1. Effects of photoperiod, temperature and vernalization and cultivar on grain yield of four South African spring wheat cultivars in controlled growth chambers.

	Photoperiod		Temperature		Vernalization		Cultivar mean grain yield (g per plant)
Wheat cultivar	11 : 13 hr	13 : 11 hr	15–5℃	20–15℃	Vern.	Unvern.	
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 columms 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; Vern., Vernalized; Unvern., Unvernalized.

producing higher yeilds than SST 86 and Carina (Table 1).

Interaction treatment effects on grain yield

The photoperiod × temperature interaction was significant due to the fact that under low temperature conditions (15–5℃) the photoperiod affected the yield more than under the warmer temperature (see Table 2a). The 13 : 11 hr/15–5℃ treatment combination resulted in the highest yield. The significant interaction between photoperiod × cultivar is shown in Table 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 × cultivar was due to large increases in grain yield of Carina (48%), 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 2c shows the significant interaction between temperature × 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℃). The significant interaction between temperature × cultivar was due to the differential decrease in grain yield under warmer temperature conditions (20–15℃).

The significant interaction between vernalization × cultivar is shown in Table 2d. Kariega and Inia produced higher grain yield following vernalization but Carina and SST 86 were unaffected by vernalization.

The significant interaction between vernalization × temperature within the 11 : 13 hr and 13 : 11 hr photoperiod treatments are shown in Table 2e. Vernalized seed in the short, cool days (11 : 13 hr/15–5℃ treatment) produced significantly higher grain yield (9.5 g per plant) while under short, warm days (11 : 13 hr/20–15℃) much lower yields were obtained (less than 2 g per plant) and was unaffected by vernalization. Under long, cool days (11 : 13 hr/15–5℃) 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 regimes (3 vs 1.9 g per plant) (see Table 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.

(2) Yield components

(i) 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 3). The temperature treatment 15–5℃ produced on average 225 per plant compared to the 20–15℃ temperature treatment at 73.5 grains per plant (Table 3).

Table 2. Significant interaction effects on grain yield per plant (g).

(a) Photoperiod and temperature

Photoperiod	Temperature 15–5℃	Temperature 20–15℃
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 and cultivar

Photoperiod	Wheat cultivar Inia	Carina	Kariega	SST 86
11 : 13 hr	5.92a	3.44a	6.97a	3.72a
13 : 11 hr	8.18b	6.68b	8.05b	6.04b
	P=0.0003	P=0.0001	P=0.0701	P=0.0002
Mean	7.05	5.06	7.51	4.88
Mean difference	−2.26	−3.24	−1.08	−2.32

(c) Temperature and cultivar

Wheat plants	Wheat cultivar Inia	Carina	Kariega	SST 86
15–5℃	10.88b	9.25b	12.36b	7.99b
20–15℃	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 and cultivar

Wheat plants	Wheat cultivar 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

(e) Vernalization, temperature and photoperiod

	(a) Short day length (Photoperiod 11 : 13 hr) Temperature		(b) Long day length (Photoperiod 13 : 11 hr) Temperature	
Wheat plants	15–5℃	20–15℃	15–5℃	20–15℃
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 is a mean of 16 observations.

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 3).

Table 3. Effects of photoperiod, temperature, vernalization and cultivar on grain number per plant of four South African wheat cultivars in controlled growth chamber conditions.

	Photoperiod		Temperature		Vernalization		Cultivar mean grain
Wheat cultivar	11 : 13 hr	13 : 11 hr	15–5℃	20–15℃	Vern.	Unvern.	number per plant
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 is a mean of 16 observations; Vern., Vernalized; Unvern., Unvernalized.

Interaction treatment effects of on grain number

The photoperiod × temperature interaction was significant for grain number (Table 4a). Wheat plants exposed to long, cool days (13 : 11 hr/15–5℃ treatment) prouduced the largest number of grains (260 grains per plant) while those under short, warm days (11 : 13 hr/20–15℃) 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℃) treatment than at the higher temperature (20–15℃) treatment.

The photoperiod × cultivar interaction is shown in Table 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. 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 × cultivar interaction was significant for grain number (see Table 4c). Inia and Kariega produced significantly higher grain number following vernalization, but Carina and SST 86 did not differ in grain number in the vernalized or unvernalized condition.

The photoperiod × temperature interaction within vernalized and unvernalized seed treatments were significant (see Table 4d). Vernalized plants reacted much more strongly to long, cool days (13 : 11 hr/15–5℃) producing significantly larger number of grains (259 per plant). Vernalized plants under short daylength

Table 4. Significant interaction effects on grain number per plant.

(a) Photoperiod and temperature

Photoperiod	Temperature 15–5℃	20–15℃
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 and cultivar

	Wheat cultivar			
Photoperiod	Inia	Carina	Kariega	SST 86
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	172.3	138.8
Mean difference	−41.5	−82.7	−18.3	−51.8

(c) Vernalization and cultivar

	Wheat cultivar			
Wheat plants	Inia	Carina	Kariega	SST 86
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, temperature and vernalization

	Vernalized Temperature		Unvernalized Temperature	
Photoperiod	15–5℃	20–15℃	15–5℃	20–15℃
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

(e) Photoperiod, cultivar and vernalization

	Vernalized Wheat cultivar				Vernalized Wheat cultivar			
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.

conditions (11 : 13 hr photoperiod) reacted much less strongly resulting in lower number of grains being obtained in the warmer temperature conditions (20–15℃), 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℃). In the warmer temperature (20–15℃) lower grain numbers were obtained (ranging between 53 and 65 grains per plant) and were 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℃), by both the vernalized and unvernalized plants, prouducing larger grain numbers (259–261 per plant) compared to the much smaller reaction of vernalized plants in the warm temperature, while unvernalized plants were unaffected by photoperiod. In general, vernalized as well as the unvernalized plants in the long, cool days (13 : 11 hr/15–5℃) resulted in higher grain numbers than short, warm day conditions (11 : 13 hr 20–15℃).

The photoperiod × vernalization × cultivar interaction was significant and is presented in Table 4e. Under vernalization Inia, Carina and SST 86 reacted strongly to long daylenth (photoperiod 13 : 11 hr treatment) prouducing 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 daylenth conditions (photoperiod 13 : 11 hr) except for Kariega under vernalization and Inia in the unvernalized state.

(ii) Mean kernel mass

Main treatment effects

Photoperiod significantly affected mean kernel mass, with the 13 : 11 hr treatment having the largest kernels averaging 37.1 g and the 11 : 13 hr treatment kernels averaging 32.1 g (Table 5). Temperature of 15–5℃ resulted in the largest mean kernel mass averaging 44.2 g and the 20–15℃ treatment the smallest kernels averaging 25.0 g (Table 5).

Vernalization significantly increased mean kernel mass, with kernels from vernalized plants averaging 35.2 g, and those from unvernalized plants averaging 34.0 g (Table 5).

Cultivar mean kernel mass, averaged over all treatments, differed with Inia and Kariega mean kernel size averaging 38.1 g, while Carina and SST 86 mean

Table 5. Effects of photoperiod, temperature, vernalization and cultivar on mean kernel mass (g) of four South African wheat cultivars in controlled growth chamber conditions.

	Photoperiod		Temperature		Vernalization		Mean kernel mass
Wheat cultivar	11 : 13 hr	13 : 11 hr	15–5℃	20–15℃	Vern.	Unvern.	(mg)
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 columms 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; Unvern., Unvernalized.

kernel size averaged 31.0 g. 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 × temperature interaction was significant (see Table 6a). At low temperature (15–5℃ treatment) photoperiod treatment did not significantly affect mean kernel mass which averaged 44.3 g, but at the high temperature (20–15℃) kernel mass increased significantly with increasing photoperiod. The 11 : 13 hr/20–15℃ treatment combination resulted in the lowest mean kernel mass averaging 20.2 g. The significant interaction was due to the difference in mean kernel mass between the two photoperiods in the warmer temperature conditions (20–15℃).

The photoperiod × vernalization interaction was significant (Table 6b). Vernalized wheat plants produced significantly larger kernels (36.5 g) under long daylength conditions (13 : 11 hr photoperiod) 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 (30.3 g). The interaction was due to the large increase in mean kernel mass (19%) in the unvernalized wheat plants compared to a 7 % kernel mass increase with vernalized wheat plants.

The photoperiod × cultivar interaction was significant and data is presented in Table 6c. The photoperiod 13 : 11 hr treatment increased significantly mean kernel mass of Carina and SST 86 but not that of Inia or 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 of Carina (44%), while for Inia and Kariega increase in mean kernel mass was comparatively small, ranging from 3.2 to 5.8% and was not significant.

The significant interaction between temperature × cultivar is shown in Table 6d, showing significant lower mean kernel mass of all the cultivars under

Table 6. Significant interaction effects on mean kernel mass (g).

(a) Photoperiod and temperature

Photoperiod	Temperature 15–5℃	Temperature 20–15℃
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

(b) Photoperiod and vernalization

Photoperiod	Wheat grain Vernalized	Wheat grain Unvernalized
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

(c) Photoperiod and cultivar

	Wheat cultivar			
Photoperiod	Inia	Carina	Kariega	SST 86
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

(d) Temperature and cultivar

	Wheat cultivar			
Temperature	Inia	Carina	Kariega	SST 86
15–5℃	46.1b	46.5b	46.2b	38.1b
20–15℃	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

(e) Photoperiod, cultivar and temperature

	Temperature 15–5℃ Wheat cultivar				Temperature 20–15℃ Wheat cultivar			
Photoperiod	Inia	Carina	Kariega	SST 86	Inia	Carina	Kariega	SST 86
11 : 13 hr	45.0a	48.2b	46.4a	36.6a	29.1a	0.0a	28.4a	23.1a
13 : 11 hr	47.2a	44.6a	45.9a	39.5a	31.3a	31.1b	31.3a	26.3b
	P=0.2690	P=0.0572	P=0.7810	P=0.1205	P=0.2487	P=0.0001	P=0.1253	P=0.0963
Mean	46.1	46.4	46.1	38.0	30.2	15.5	29.8	24.6
Mean difference	−2.2	3.6	0.5	−2.9	−2.9	−31.1	−2.8	−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.

warmer temperature conditions (20–15℃). In real terms, the interaction was due to the large decrease in mean kernel mass of Carina (66%) compared to small but significant decreases by Inia (34%), Kariega (35%) and SST 86 (35%).

The photoperiod × cultivar × temperature interaction was significant as shown in Table 6e. Within the 15–5℃ 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℃ temperature treatment Inia and Kariega did not differ in mean kernel mass in both photoperiod treatment conditions. Carina did not produce any grains in the short, warm days (11 : 13 hr/20–15℃ treatment), but in the long, warm days (13 : 11 hr/20–15℃) its kernels averaged 31.1 g. The sensitivity of Carina to warmer temperature conditions was indicated by its inability to produce any grains under short, warm days (11 : 13 hr/20–15℃) 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.

(iii) 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% protein (Table 7).

Temperature differences did not result in significant differences in grain protein content, neither had vernalization any effect. The cultivars differed in grain proteint content with Inia at 19% significantly higher than Carina (14.5%) and Kariega (15.9%) (see Table 7). The cultivar Carina produced no yield under short, warm days conditions (11 : 13 hr/20–15℃ treatment) and hence, yield averaged over other treatments (see Tables 1, 7, 8a and 8b).

Table 7. Effects of photoperiod, temperature, vernalization and cultivar on percentage grain protein content of four South African wheat cultivars in growth chambers.

Wheat cultivar	Photoperiod		Temperature		Vernalization		Cultivar mean grain yield (g per plant)
	11 : 13 hr	13 : 11 hr	15–5℃	20–15℃	Vern.	Unvern.	
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 columms followed by the same letter are not significantly different according to Fisher's test ($P \leq 0.05$). Each value is a mean of 8 observations ; Vern., Vernalized ; Unvern., Unvernalized.

*Carina data averaged over treatments (13 : 11 hr/15–5℃ ; 13 : 11 hr/20–15℃ and 11 : 13 hr/15–5℃ due to treatment 11 : 13 hr/20–15℃ producing no yield.

Interaction treatment effects on grain protein content

The photoperiod × cultivar interaction was significant (see Table 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) 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℃ treatment). The significant interaction was due to significant increase in grain protein content of Inia between the two photoperiod treatments.

The photoperiod × temperature × cultivar interaction was significant and is presented in Table 8b. Within the 11 : 13 hr photoperiod treatment Inia, Kariega and SST 86 did not significantly differ in grain protein content under the two temperatures (15–5℃ or 20–15℃ treatment). Comparison is not made between cool (15–5℃ temperature) and warm (20–15℃ temperature) treatment conditions because Carina had no yields under short, warm days (11 : 13 hr/20–15℃ 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℃ treatment) significantly decreased grain protein content by about 31% while that of Carina increased in the 20–15℃ 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 × temperature × cultivar no further explanation is attempted.

Table 8. Significant interaction effects on percentage grain protein content.

(a) Photoperiod and cultivar

	Wheat cultivar			
Photoperiod	Inia	Carina	Kariega	SST 86
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

(b) Temperature, cultivar and photoperiod

	Photoperiod 11 : 13 hr Wheat cultivar				Photoperiod 13 : 11 hr Wheat cultivar			
Temperature	Inia	Carina	Kariega	SST 86	Inia	Carina	Kariega	SST 86
15–5℃	15.1a	16.1b	14.6a	15.8a	26.1b	16.9a	15.9a	15.2a
20–15℃	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 columms 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.

*No yield obtained from Carina in treatment 11 : 13 hr/20–15℃.

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

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 (*22, 10, 11*).

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℃/vernalization treatment conditions. These plant variables were significantly increased under conditions of long daylength, cool temperatures and vernalization. Grain yields were higher at low temperatures and associated with a longer period of grain growth, while higher temperatures results in lower grain yields (*30*). Similar results for various temperatures imposed during grain-filling have been reported (*33, 35*). Plants grown under long daylength and low temperature (13 : 11 hr/15–5℃ treatment) produced higher grain yields and grain protein content than those exposed to short daylengths and low temperature conditions (11 : 13 hr/15–5℃ treatment) (Table 1). It has been shown in the field that high temperatures during the grain-filling period can limit grain yield and higher grain quality (*17, 31*). Experiments under controlled environmental conditions have shown that high temperatures can reduce yield because individual kernel weights are lower (*15, 31*). Grain quality may be reduced or enhanced by high temperature during grain development depending on cultivar and growth environmental conditions (*5*). For example, it was reported that higher temperatures increased grain protein content levels in the cultivar Schirokko (*28*).

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 is increased by cool temperature and long photoperiod (*22, 6*). 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 the cold treatment and temperature conditions, while potential yield may not be realised because of unfulfilled vernalization requirements (*4, 12, 24, 37*). 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 (*18*) and (*19*). 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 with 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 unmber 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.

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