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GROWTH AND YIELD COMPONENTS OF WHEAT GENOTYPES EXPOSED TO HIGH TEMPERATURE STRESS UNDER CONTROL ENVIRONMENT

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Abstract

High temperature stress during grain-filling period is one of the major environmental constraints limiting the grain yield of wheat in Bangladesh. Crop growth response and relative performance of yield components of ten wheat genotypes were studied in two temperature conditions in glass rooms in a Phytotron to identify the genotype tolerant to high temperature stress. A favourable day/night temperatures of 15/10, 20/15, and 25/20 °C were maintained from sowing to 60 days after sowing (DAS), 61 to 80 DAS and 81 DAS to maturity, respectively, in one glass room (G1); whereas day/night temperatures in another glass room (G_2) was always maintained at 5°C higher than that of G₁. Green leaf area and number of tillers in different times, number of days for the occurrence of major crop growth stages, relative performance in yield components, grain yield and heat susceptibility index were estimated following the standard methods. The higher temperature enhanced plant growth, flowering, and maturation. Thus the number of days to booting, heading, anthesis, and maturity of wheat were significantly decreased that varied among the genotypes. Green leaf area and productive tillers/plant were drastically reduced in time under high temperature. The reduced number of grains/spike and smaller grain size resulted from drastic reduction in growth duration were responsible for the yield loss of wheat at high temperature. Out of ten wheat genotypes, three were characterized as high temperature tolerant based on their relative performance in yield components, grain yield and heat susceptibility index.

Key Words: High-temperature tolerance, wheat genotype, growth and yield components.

Introduction

The optimum temperature for the growth and development of spring-wheat is around 20°C (Paulsen, 1994), but the temperature often rises above 30°C before the physiological maturity of wheat in many wheat growing countries including Bangladesh. High temperature during the reproductive stage and grain-filling is one of the main causes of yield loss in late-sown wheat in Bangladesh (Ahmed

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and Maisner, 1996). Field experimental results suggested that high temperature stress had the potential to reduce grain yield of wheat by two to four folds (Shipler and Blum, 1986; Zhong-hu and Rajaram, 1994). The crop may be exposed to more thermal stress in the near future, as it is predicted that the global warming may cause a temperature increase of about $2^{\circ}C$ by the middle of twenty-first century (Karttenberg et al., 1995). The relationship of high temperature to wheat yield was intensively studied by several authors and in general, the yield was reported negatively correlated to higher temperature (Wheeler et al., 1996 and Batts et al., 1997) and particularly, the reproductive stage is more vulnerable to high temperature (Stone and Nicolas, 1995; Gibson and Paulsen, 1999). The yield reduction of wheat under high temperatures is associated with a less number of grains/spike and smaller grain size (Gibson and Paulsen, 1999) and there are variations among cultivars in response to high temperature (Wardlaw and Moncur, 1995). Also higher temperature enhances leaf senescence causing reduction in green leaf area during reproductive stages. The rapid leaf senescence ultimately resulted in less productive tillers/plant, which is one of the major causes of yield loss of wheat. However, crop response to high temperatures varied with variation of temperatures, duration of exposure, crop growth stages, and also due to the level of crop tolerance. There are several major aspects of thermo-tolerance from the biochemical and metabolic levels, the relation to membrane stability, production of heat shock proteins, and productivity during high temperature stress. The present study deals with green leaf area, crop growth stages, relative performance of yield components and yield of ten diverse wheat genotypes in contrast temperatures in order to identify the genotypes relatively tolerant to high temperature at whole plant level on the basis of crop productivity.

Materials and Method

The experiments were conducted under two thermal conditions in two glass rooms in the Phytotron, at the Biotron Institute in Kyushu University, Japan. Day/night temperatures of 15/10, 20/15, and 25/20°C were maintained from sowing to 60 days after sowing (DAS), 61-80 DAS and 81 DAS to maturity, respectively, in one glass room (G₁). In contrast, day/night temperatures in another glass room (G₂) were always maintained at 5°C higher than G₁ mentioned above. The whole package of temperature treatments maintained in G₁ and G₂ were referred to as optimum temperature (OPT) and high temperature (HT), respectively, in the rest of this paper. Ten spring- type elite wheat lines and cultivars from different sources were tested in this study. The variety Kanchan and four advanced lines viz., BAW-969, SW89-5124*21FASAN, W 82/VEE/KOEL 1 3/PEG//MLR/BUC and HP/ 1731 from Wheat Research Centre of Bangladesh Agricultural Research Institute and four lines viz., SERI/ RAYON, LAJ 3302/2* M088, BORL 95/ LAJ 3302, and OASS/SKAUZ// 4*BCN collected from CIMMYT, Mexico and one

Zimbabwean variety SCAN with good yield potentials were used in this study. In the rest of this paper, the aforementioned 10 wheat genotypes are denoted numerically in sequence from W-1 to W-10 with the sign of source country as: B for Bangladesh, M for CIMMYT, Mexico and Z for Zimbabwe for the convenience of presentation. Plastic pots, 19 cm in height and 16 cm in diameter, with a drainage facility were filled with 4 kg of air-dried ground and sieved soils (<2.0 mm) and were used as the growth media. Basal fertilizers of N, P, and K were applied at the rate of 40, 30, and 30 mg/kg of soil, respectively. The soil was thoroughly mixed before being poured into the pots and the pots were arranged in each glass room in three rows assuming 3 replications of 10 pots. Seeds of ten wheat genotypes were sown in 10 pots randomly thus the study considered as a two factor (Temperature and Genotype) experiment laid out in randomized complete block design. Before sowing seed, the moisture condition of soils of all the pots was set around field capacity (30-31% by volume). Soil moisture was regularly monitored by TDR (Time domain reflectometry) method following Topp et al. (1980) to ensure uniform water supply in all the pots. After germination, five healthy seedlings were allowed to grow in each pot. Nitrogen from ammonium chloride was also applied at the rate of 20 mg/kg of soil with irrigation water at 25 and 35 DAS. The crops in both the glass rooms were exposed to uncontrolled natural light with controlled relative humidity of 70%. All other environmental and management conditions were similar in both the glass rooms. All the plants in both the glass rooms were under keen observation to note the accurate dates of the plant growth stages of booting, heading, anthesis, and maturity. Zadoks' scale (Zadoks et al., 1974) was followed to denote the aforementioned growth stages as the scale is described as the most comprehensive and easiest scale that provides a good description for both vegetative and reproductive stages (Harrel et al., 1993). Destructive samplings of plants were made in 5 different times of 50 DAS, at anthesis, 10 days after anthesis (DAA), 20 DAA, and at maturity. After sampling, the above-ground plant parts were segmented into different components of leaf, culm, spike, and grain. Leaf area was measured by an automatic leaf area meter (Model: AAM-8, Hayashi Denko, Tokyo) immediately after sampling the plant. After measuring the leaf areas, plant components were oven-dried at 70° C for 72 hours and weighed to determine dry matter weight. The number of tillers per plant was also counted at different stages of 30, 50, 70, and 90 DAS. Yield components of grains/spike, grain weight (mg/kernel) and grain yield (g/plant) were determined after harvest. To compare the performance of a genotype, relative performance (RP%) for yield and yield components were calculated as follows:

RP% = (Yield performance under HT/Yield performance under OPT) x 100.

Heat susceptibility index (S) was calculated for grain yield using the following equation as described by Fisher and Maurer (1978):

S = (1 - Y/Yp), 1(1 - X/Xp)

Where, Y is mean grain yield of a genotype under stress environment (high temperature), Yp is mean yield of the same genotype under stress free environment (optimum temperature), X is mean Y of all genotypes, and Xp is mean Yp of all genotypes. If S < 0.5, the crop is highly stress tolerant, if S > 0.5 < 1.0, moderately stress tolerant, and if S > 1.0, susceptible to stress. All the data were statistically analyzed and means were compared by least significant difference (LSD) test at 5% level of probability.

Results and Discussion

Leaf area

Leaf area (LA) of wheat largely depends on the diversity of genotype, plant growth stage and air temperature. At early growth stages until 50 DAS, LA was higher under HT compared to OPT for all the genotypes, but at later stages, the trend was reversed (Fig. 1). Leaf senescence enhanced by higher temperature caused reduction in green leaf area resulting in drastic reduction in LA at later stages of 10 DAA and 20 DAA in HT and the trend was common for all the genotypes. However, there were variations among the genotypes both for HT and OPT conditions. Particularly under HT at 20 DAA, the LA of BW-3, BW-4, and MW-8 was higher than other genotypes indicating that these three genotypes were relatively tolerant to high temperature induced leaf senescence. Larger LA at later stages might contribute to higher photosynthesis that ultimately resulted in higher grain yields. Genotypic difference in green leaf area duration in response to heat stress is also reported by Stone and Nicolas (1998); and Fisher et al. (1998). High temperature induced leaf senescence largely depends on membrane thermo-stability which varied with varietal tolerance. In heat tolerant cultivars, leaf senescence is reported to occur after significant grain growth, while in sensitive cultivars, leaf senescence occur before substantial grain growth (Rahman et al., 2005). Modem wheat varieties possess the highest leaf area at or near the booting stage and afterward decrease due to the loss of green plant tissue (Calderini et al., 1997). Cao and Moss (1989) and Acevedo et al. (1991) reported that total number of leaves and leaf area were reduced differently in different wheat genotypes in response to high temperature stress. In present study, it was observed that the flag leaves of some of the genotypes expanded lately but they senesced at the same time with others where flag leaf expanded earlier resulting a shorter leaf area duration in those genotypes.

Number of tillers/plant

Initially at 30 DAS, number of tillers/plant of different wheat genotypes was similar to both the thermal conditions of OPT and HT, but significant differences

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Fig. 1. Effect of temperature on leaf areas of 10 wheat genotypes at 3 different growth stages (DAS-Days after sowing, DAA- Days after anthesis, OPT- Optimum day/night temperatures of 15/10, 20/15, and 25/20°C were maintained from sowing to 60 DAS, 61-80 DAS and 81 *DAS* to maturity, HT- Higher day/night temperature of 5° C over OPT, Error bar indicates LSD at 5% level of significance to compare varietal response at 3 growth stages).

were found at and after 50 DAS. Number of tillers/plant was maximum at late vegetative stage of 50 DAS for all the wheat genotypes and thereafter at 70 and 90 DAS, the number of productive tillers/plant was significantly reduced and the reduction was higher in HT compared to OPT conditions for all genotypes (Table 1). It was due to survival of only a few productive-tillers/plant at higher temperatures. Under HT, the genotypes of BW-3 and MW-8 produced the maximum number of tillers at 50 DAS whereas BW-4 produced the highest number of productive tillers at 90 DAS. Under OPT condition, the genotype ZW-10 produced higher number of tillers at 50, 70, and 90 DAS compared to other genotypes. The same genotype survived with the least number of productive tillers/plant at 90 DAS under HT indicating that the survival of late tillers of this genotype was severely affected by higher temperature. Again, the genotype BW-4 produced comparatively less number of tillers at 50, 70, and 90 DAS under OPT; but under HT, the genotype survived with comparatively high number of productive tillers/plant at later stage of 90 DAS. The result indicated that survival of tillers of BW-4 was relatively less affected by higher temperature. In general, it was observed that plants of all the wheat genotypes grew faster with few number of tillers/plant under HT, whereas the same genotype grown slowly with

comparatively good number of tillers/plant under OPT. Several reports suggest that the ability to producing tillers of wheat plant and their survival depends on genotype, spacing, agronomic and nutritional management practices, and also on environmental factors, especially air temperatures (Kirby *et al.*, 1985; Longnecker *et al.*, 1993). Stern and Kirby (1979) described tiller initiation process in the axils of the basal leaves of wheat plant and reported that under unfavourable environment, the growth of tiller slows or stops depending on variety. Fisher (1985) also reported that high temperature stress inhibited the initiation and survival of tiller in wheat plant.

 Table 1. Effect of temperature on number of tillers/plant of wheat genotypes over time.

Genotypes	30 DAS		50 DAS		70 DAS		90 DAS	
	OPT	HT	OPT	HT	OPT	HT	OPT	HT
BW-1	2.87	2.87	5.73	4.64	3.87	2.64	2.33	1.67
BW-2	2.67	2.67	4.23	4	3.34	2.53	2.67	1.67
BW-3	2.67	2.87	5.67	5.1	3.97	2.38	2.67	1.87
BW-4	2.8	2.33	3.67	3.33	3.41	2.67	2.33	2.33
BW-5	2.33	2.28	4.33	3.73	3.18	2.49	2.5	1.77
MW-6	2.67	2.67	5.2	4.3	3.72	2.41	2.5	1.67
MW-7	2.8	2.93	5.67	4.67	4.33	2.56	2.87	1.6
MW-8	2.8	2.8	5.87	5.4	4.22	2.95	2.87	1.87
MW-9	2.33	2.67	5.33	4.47	3.77	2.61	2.53	1.87
ZW-10	2.83	2.33	6.33	4.47	4.75	2.28	3.33	1.33
LSD (0.5)	ns	ns	0.82	0.58	0.46	0.46	0.46	0.21
CV (%)	7.24	10.12	6.5	9.25	7.24	7.14	6.11	7.21

DAS-Days after sowing, OPT- Optimum day/night temperatures of 15/10, 20/15, and $25/20^{\circ}$ C were maintained from sowing to 60 DAS, 6 1-80 DAS and 81 DAS to maturity, HT- Higher day/night temperature of 5° C over OPT.

Growth stages

Since higher temperature enhanced plant growth and forced the maturity, the different growth and development stages of all the wheat genotypes occurred earlier in HT compared to OPT condition (Table 2). In both the thermal conditions, plant growth of the genotypes showed small differences in early vegetative stages (data not shown) but at and after the onset of stem elongation, significant differences were found among the genotypes. Therefore, the number of days to booting, heading, anthesis, and maturity of wheat varied significantly due to genotypic variations. Booting, heading, anthesis, and maturity of wheat

genotypes denoted as Zadoks' growth stage of 4.5, 5.5, 6.5, and 9.4 occurred 15 to 21, 17.4 to 22.7, 18 to 26, and 27.6 to 42.7 days earlier, respectively, in HT as compared OPT condition. Under HT, the days to booting, heading, anthesis, and maturity of BW-1 were the minimum and were statistically similar to those of BW-2, BW-5, and MW-6. Whereas the aforementioned growth stages of wheat occurred lately in case of genotypes BW-3, BW-4, and MW-8. Also the plants of these three genotypes get relatively wid grain growth duration (anthesis to maturity) that may contribute to the grain size (Table 3). Number of days to maturity was maximum (137.7 d) for the genotype ZW-10 under OPT and the same genotype matured in minimum days (95 d) under HT. The difference in number of days to maturity between OPT and HT was maximum in ZW- 10, and minimum in BW-3. The result indicated that growth stages of ZW- 10 was the most sensitive to higher temperature stress whereas the growth stage of BW-3 was relatively tolerant to higher temperature stress. Environmental effect on the number of days required for the occurrence of different growth stages of wheat varied with genotypes (Araus et al., 2007).

 Table 2. Number of days from seeding to booting, heading, anthesis and maturity of wheat genotypes under contrast temperatures.

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Genotypes	Booting		Heading		Anthesis		Maturity	
	(Zadoks'	stage 4.5)	(Zadoks'	stage 5.5) (Zadoks'		stage 6.5)	(Zadoks' stage 9.4)	
	OPT	HT	OPT	HT	OPT	HT	OPT	HT
BW-1	74.3	57	82	62.7	88.7	68.3	126.3	95.3
BW-2	74.7	57.3	82.3	62.7	88.7	68.7	125.7	95.3
BW-3	77.3	62.3	86.3	68.7	90.7	72.7	129.3	101.7
BW-4	78	63.7	87.3	68	92.7	72.7	129	99.3
BW-5	79.3	59	89.7	64.3	94.7	68	132.7	95.7
MW-6	76	57	85.7	62	91.3	67	128	95.3
MW-7	82.3	61.3	88.3	67.7	93.7	71	130.7	98.3
MW-8	80.7	64	87.7	69	94.7	72	129.7	101.3
MW-9	78.3	60.7	85.7	66.7	91	71.3	128	96.7
ZW-10	85.7	64.7	93	70.3	99.7	74.7	137.7	95
LSD (0.5)	5.8	4.1	5.3	3.9	6.3	4.2	7.3	5.1
CV (%)	6.25	4.11	7.6	5.21	7.11	6.1	5.81	5.3

OPT- Optimum day/night temperatures of 15/10, 20/15, and 25/20 0 C were maintained from sowing to 60 DAS, 61-80 DAS and 81 DAS to maturity, HT- Higher day/night temperature of 5 0 C over OPT.

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Genotypes	Grains/spike			Grain weight (mg/kernel)				
	OPT	HT	RP (%)	OPT	HT	RP (%)		
BW-1	41.9	34.3	81.9	48.9	39.7	81.2		
BW-2	41	32.7	79.8	49.1	40.1	81.7		
BW-3	52.8	45.3	85.8	49.7	42.1	84.7		
BW-4	50.3	43.3	86.1	48.8	42.7	87.5		
BW-5	51.2	36	70.3	45.1	32.1	71.2		
MW-6	49.2	35.3	71.7	45.8	28	61.1		
MW-7	43.3	33.4	77.1	39.8	28.5	71.6		
MW-8	48.7	42.3	86.9	49.7	40.5	81.5		
MW-9	50.7	37.3	73.6	42.7	33	77.3		
ZW-10	53.3	33.1	62.1	41.9	28	66.8		
LSD (0.05)	4.1	3.7		3.9	2.5			
CV (%)	6.4	6.8		6.5	6.2			

 Table 3. Number of grains/spike and grain weight of wheat genotypes under contrast temperatures.

OPT- Optimum day/night temperatures of 15/10, 20/15 and 25/20° C were maintained from sowing to 60 DAS, 61-80 DAS and 81 DAS to maturity, HT- Higher day/night temperature of 5°C over OPT, RP — Relative performance.

Relative performance in yield components

High temperature reduced the number of grains/spike, which varied among the genotypes for both the temperature conditions (Table 3). The relative performance (RP %) of grains/spike varied from 87.1% in BW-2 to 62.1% in ZW-10, indicating that high temperature of 5°C reduced grain number from 12.9 to 37.9% depending on wheat genotype. Stone and Nicolas (1995) and Gibson and Paulsen (1999) also reported the genotypic difference of grains/spike in response to high temperature. High temperature may affect the pollen viability and fertilization and thereby reduce the number of grains/spike. Individual grain weight which considered as one of the major yield contributor was also significantly influenced by temperature. Higher temperature enhanced plant maturation (Table 2) causing reduction in grain growth duration (Rahman et al., 2005) which ultimately resulted in smaller grains. However, significant differences in grain weight (mg/kernel) were found among the genotypes both for OPT and HT conditions. Though the genotypes BW-1, BW-2, BW-3, BW-4, BW-5, and MW-8 produced similar grain weight under OPT, but under HT only three genotypes BW-3, BW-4, and MW-8 performed the best result (Table 3). RP (%) for the grain weight varied from 61.1% in MW-6 to 87.5% in BW-4. The result

revealed that weight of matured wheat grain reduced by 12.5 to 38.9% due to higher temperature of 5° C above the optimum. Rahman *et al.* (2005) reported that higher temperature (30/20° C, day/night) induced significant reduction of final grain weight, grain growth rate and grain growth duration of wheat as compared to optimum temperature (25/15 °C, day/night). Hawker and Jenner (1993), and Wallwork *et al.* (1998) apprehended that high temperature injuries were due to disappearance of enzyme activity relating to starch synthesis in the grains of wheat and barley, respectively. Similar adverse effect of higher temperature on kernel development and grain filling rate of wheat is reported by Gibson and Paulsen (1999); Viswanathan and Chopra (2001).

 Table 4. Effect of temperatures on biomass, grain yield and heat susceptibility index of wheat genotypes.

Genotypes	Biomass (g/plant)			Grain yield (g/plant)				
	OPT	HT	RP (%)	OPT	HT	RP (%)	HSI	
BW-1	10.3	5.8	55.7	4.1	2.2	52.9	0.97	
BW-2	11.1	5.9	53.3	4.2	2.5	58.5	0.87	
BW-3	11.0	6.8	62.3	4.6	3.0	64.7	0.74	
BW-4	11.6	7.1	61.1	4.5	2.8	62.6	0.75	
BW-5	11.8	5.4	45.5	4.3	1.9	44.7	1.16	
MW-6	11.0	4.6	41.8	3.8	1.4	36.4	1.33	
MW-7	10.4	5.5	52.5	3.7	1.8	49.8	1.05	
MW-8	11.8	7.2	60.9	4.4	2.8	65.0	0.73	
MW-9	10.4	5.9	56.5	3.8	2.1	55.5	0.93	
ZW-10	12.3	5.2	42.4	5.1	1.7	32.5	1.41	
LSD (0.5)	1.7	1.2		0.4	0.6			
CV (%)	8.81	7.11		8.56	6.67			

OPT- Optimum day/night temperatures of 15/10, 20/15 and 25/20 $^{\circ}$ C were maintained from sowing to 60 DAS, 61-80 DAS and 81 DAS to maturity, HT- Higher day/night temperature of 5 $^{\circ}$ C over OPT, RP — Relative, performance, HSI — Heat susceptibility index.

Relative yield and heat susceptibility index

The final biomass and grain yield of all the wheat genotypes significantly decreased in HT compared to OPT. However, there were significant differences among the genotypes in grain yield and biomass production for both thermal conditions (Table 4). Under OPT, the final biomass of the genotype ZW-10 was the highest which was similar to BW-2, BW-3, BW-4, BW5, and MW-8, but significantly higher than BW-1, MW-7, and MW-8. This trend of biomass

production of the genotypes was altered under HT, where MW-8 produced the highest biomass. The genotype BW-3 and BW-4 also produced high biomass, which was statistically identical to MW-8, but higher than other genotypes. The relative performance in biomass production indicated maximum biomass loss in MW-6 and minimum loss in BW-3 due to high temperature. Like biomass, grain yield of the genotype ZW- 10 was the highest under OPT and the same genotype had the lowest RP in grain yield of 32.5%, with the highest S value of 1.41 indicating that ZW-10 is highly susceptible to high temperature. Heat susceptibility indices of MW-7, MW- 6, and BW-5 were higher than 1.0, indicating that these genotypes also had no tolerance to high temperature. The S values of the other six wheat genotypes, MW-8, BW-4, and BW-3 had lower S values less than 0.80 that characterized their relatively high tolerance to high temperature.

Conclusion

Crop growth, growing periods, grain yield and all the yield components of wheat genotypes were affected by high temperature. Different genotypes showed variable response to high temperature. With respect to relative performance in yield components and heat susceptibility index, three genotypes MW-8, BW-4, and BW-3 were characterized as moderately tolerant to high temperature. The tolerant lines had relatively high leaf area, and wider growing period under heat stress. The aforementioned three wheat lines had the potentials to be used as the variety under the warmer environment and could be used in breeding programme to develop heat tolerant wheat variety.

References

- Acevedo, E., M. Nachit and G. Ortiz-Ferrara. 1991. Effects of heat stress on wheat and possible selection tools for use in breeding for tolerance. *In:* D.A Saunders, ed. *Wheat for the non-traditional warm areas*, p. 401-421. Mexico, DF, CIMMYT.
- Ahmed, S. M. and C. A. Meisner. 1996. Wheat Research and Development in Bangladesh. Bangladesh- Australia Wheat Improvement Project and CIMMYT-Bangladesh, Dkaka, pp. 201.
- Araus, J., J.Ferrio, R. Buxo and J. Voltas. 2007. The historical perspective of dryland agriculture: lessons learned from 10 000 years of wheat cultivation. J. Exp. Bot. 58(2): 131 - 145.
- Batts, G. R., J. I. L. Morison, R. H. Ellis, P. Hadley and T. R. Wheeler. 1997. Effect of CO₂ and temperature on growth and yield of crops of winter wheat over four seasons. *European J Agron.* 7: 43-52.
- Calderini, D.F., M.F. Dreccer and G.A. Slafer. 1997. Consequences of breeding on biomass, radiation interception and radiation-use efficiency in wheat. *Field Crops Res.* **52**: 271-281.

- Cao, W. and D. N. Moss. 1989. Temperature effect on leaf emergence and phyllochron in wheat and barley. *Crop Sci.* 29: 1018-1021.
- Fischer, R.A. 1985. Number of kernels in wheat crops and the influence of solar radiation and temperature. *J. Agric. Sci.* **105**: 447-461.
- Fisher, R. A., D. Rees, K. D. Sayre, Z. M. Lu, A. G. Condon, and A. L. Savedra. 1998. Wheat yield progress associated with higher stomatal conductance and photosynthetic rate, and cooler canopies. *Crop Sci.* **38**: 1467-1475.
- Fischer, R. A. and R. Maurer. 1978. Drought resistance in spring wheat cultivars. I. Grain yield responses. *Aust. J. Agric. Res.* **29:**897-912.
- Gibson, L. R., and G. M. Paulsen. 1999. Yield components of wheat grown under high temperature stress during reproductive growth. *Crop Sc.* **39**: 1841-1846.
- Harrel, D.M., W.W. Wilhelm and G. S. McMaster. 1993. SCALES: a computer program to convert among three developmental stage scales for wheat. *Agron. J.* 85: 758-763.
- Hawker, J. S. and D. F. Jenner. 1993. High temperature affects the activity of enzymes in the committed pathway of starch synthesis in developing wheat endosperm. *Aust. J. Plant Physiol.* **20**: 197-209.
- Karttenberg, A. F., H. Giorgi, G. A. Grassl, J. F. B. Meehl, R. J. Mitchll, T. Stouffer, A. Tokioka, J. Weaver and T. M. L. Wigley. *1995. Climate models-projection of future climate. In:* Houghton, J. T. ed. "The science of climate change. Contribution of working group I to the second assessment report of the intergovernmental panel on climate change". Cambridge University, Cambridge, pp. 289-357.
- Kirby, E.J.M., M. Appleyard and 0. Fellowes. 1985. Variation in development of wheat and barley in response to sowing date and variety. J. Agric. Sc. 104: 383-396
- Longnecker, N., E. J. M. Kirby and A. Robson. 1993. Leaf emergence, tiller growth, and apical development of nitrogen-deficient spring wheat. *Crop Sc.* **33**: 154-160.
- Paulsen, G. M. 1994. High temperature responses of crop plant. In: "Physiology and determination of crop yield" (ed. by Boote, K. J.). ASA, CSSA, SSSA, Madison, WI, pp. 365-389.
- Rahman, M. A., J. Chikushi, S. Yoshida, H. Yahata and B. Yasunsga. 2005. Effect of high air temperature on grain growth and yields of wheat genotypes differing in heat tolerance. J. Agric. Meteorol. 60: 605-608.
- Shipler, L. and A. Blum. 1986. Differential reaction of wheat cultivars to hot environments. *Euphytica* **35**: 483-492.
- Stern, W.R. and E.J.M. Kirby. 1979. Primordium initiation at the shoot apex in four contrasting varieties of spring wheat in response to sowing date. J. Agric. Sci. 93: 203-215.
- Stone, P. J. and M. E. Nicolas. 1995. A survey of the effects of high temperature during grain filling on yield and quality of 75 wheat cultivars. *Aust. J. Agric.Res.* **46**: 475-492.
- Stone, P. J. and M. E. Nicolas. 1998. The effect of duration of heat stress during grain filling on two wheat varieties differing in heat tolerance: Grain growth and fractional protein accumulation. *Aust. J. Plant Physiol.* 25: 13-20.

- Topp, G. C., J. L. Davis, and A. P. Annan. 1980. Electromagnetic determination of soil water content: Measurements in coaxial transmission lines. *Water Resource Res.* 16: 574-582.
- Viswanathan, C. and R. K. Chopra. 2001. Effect of heat stress on grain growth, starch synthesis and protein synthesis in grains of wheat varieties differing in grain weight stability. I. *Agron.* & *Crop Sc.* **186**: 1-7.
- Wallwork, M. A. B., S. J. Logue, L. C. MacLeod, and C. F. Jenner. 1998. Effect of high temperature during grain filling on starch synthesis in developing barley grain. *Aust. J. Plant Physiol.* 25: 173-181.
- Wardlaw, I. F. and L. Moncur. 1995. The response of wheat to high temperature following anthesis. I. The rate and duration of kernel filling. *Aust. J. Plant Physiol.* 22: 39 1-397.
- Wheeler, R. L., G. R. Batts, R. H. Ellis, P. Hadley, and J. 1. L. Morison. 1996. The duration and rate of grain growth and harvest index of wheat (*Triticum aestivum*) in response to temperature and CO₂. J. Expt. Botany 47: 623-630.
- Zadoks, J.C., T.T. Chang and C. F. Konzak. 1974. A decimal code for the growth stages of cereals. *Weed Res.* 14: 415-421.
- Zhong-hu, H. and S. Rajaram. 1994. Differential responses of bread wheat characters to high temperature. *Euphytica* **72**: 197-203.