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IRRIGATION AND NITROGEN EFFECTS ON GRAIN DEVELOPMENT AND YIELD IN WHEAT (*TRITICUM AESTIVUM* L.)

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Abstract

A field study was conducted to determine the effects of different levels of irrigation and nitrogen on grain development (grain filling rate and grain filling duration) and grain yield of wheat (*Triticum aestivum* L.) variety Inqlab-91. The experiment was conducted at the Crop Physiology research area, University of Agriculture, Faisalabad, Pakistan, during the year 2002-03 and 2003-04. Four irrigation levels i,e one irrigation (Irrigation at tillering stage), two irrigations (irrigations at tillering and anthesis stages), three irrigations (irrigations at tillering, anthesis and grain development stages), four irrigations (irrigations at tillering, stem elongation, anthesis and grain development stages) and four nitrogen levels i.e, 0, 50, 100 and 150 kg N ha^{-1} were tested in this study. Grain yield and all primary yield components increased linearly in response to irrigation and nitrogen in both seasons. Grain yield, number of spikes m^{-2}, grains $spike^{-1}$ and grain weight responses were greater at the higher N rates. Mean grain yield in four, three and two irrigation treatments compared with that in one irrigation treatment increased by 47, 23 and 9% during 2002-03 and 91, 84 and 23% in 2003-04, respectively. Water deficit reduced spikes m^{-2}. In both years, the average reductions in spikes m^{-2} and grains $spike^{-1}$ in one irrigation treatment at all N levels were 24% and 36%, respectively. Decreasing number of irrigation accelerated the GFR and hastened the GFD, whereas N application increased GFR and duration at all irrigation levels. Reduction in grain yield under less irrigation treatment is the result of a significant reduction in number of effective tillers and nitrogen supply improved effective tillers per unit area at all irrigation levels.

Introduction

Grain development is a function of rate and duration of grain growth, determined by photosythates supply and is affected by a number of environmental factors including water and nitrogen. Water stress and nitrogen deficiencies reduce photosythates production because of stomatal closure and early senescence (Singh & Wilkens, 1999) which ultimately affect grain development processes. The effect of water and nitrogen on physiological responses in wheat indicates that supplemental water is needed for high rates of spring applied N to increase the rate and duration of leaf photosynthesis in winter wheat during grain filling period (Frederick & Camberato, 1994).

Water stress and nitrogen deficiencies during the vegetative phase can cause early senescence and maturity. During grain development N stress shortens the duration of grain filling (Singh & Wilkens, 1999). Yang *et al*., (2000) studied the effect of two levels of nitrogen, normal (NN) or high (HN), applied at heading and controlled soil drying imposed 9 days after anthesis until maturity. They observed that soil drying shortened the grain filling period but the nitrogen application along with soil drying substantially increased grain filling period except in severe soil drying treatments. The influence of different doses of nitrogen (60, 120, 180, kg/ha) on grain filling, grain yield and yield components of wheat (*Triticum aestivum* L.) under warm dry conditions indicates that grain development in lower part of spike responded more to nitrogen. However, grain-filling duration remained unchanged at all levels of nitrogen (Ahmad *et al*., 1988).

Higher grain weight of well-watered plants are associated with longer grain filling duration and faster grain filling rate (Li *et al*., 2000). Water stress-induced accelerated senescence after anthesis shortens the duration of grain filling by causing premature desiccation of the endosperm and by limiting embryo volume has also been reported (Westage, 1994). The objective of this study therefore was to study the interactive effect of different levels of irrigation and nitrogen on grain development in wheat.

Materials and Methods

Two field experiments were conducted during November-April 2002-03 and 2003-04 on a sandy loam soil at the Department of Crop Physiology, University of Agriculture, Faisalabad, Pakistan (31.25^0 N latitude, 73.09^0 E longitude and 184 m altitude). The climate of the experimental site is characterized by a semi-arid with hot dry summer and severe cold winter seasons. Mean maximum temperature for the wheat-growing season was 26°C in 2002-03 and 29°C in 2003-04 (Figs. 1 and 2). Before sowing soil test showed organic matter content from 0.60 to 0.73% and N 0.031-0.037%, P_2O_5 5.0-5.6 ppm and K_2O 161-175 ppm in both the seasons (Table 1). Soil samples were analyzed according to the method given in US Salinity Hand Book No. 60 (Anon., 1954) except available P and soil texture, which were determined by methods described by Watanabe & Olsen, (1965) and Moodie *et al*., (1959), respectively.

Four irrigation and nitrogen treatments were applied for the study. Irrigation treatments included: One irrigation at tillering stage (I_1); two irrigations at tillering and anthesis stages (I_2); three irrigations at tillering, stem elongation and grain development stages (I_3); four irrigations at tillering, stem elongation, anthesis and grain development stages (I_4). Amount of water applied per irrigation was 76.4 mm. The total water applied (irrigation + rainfall) for each water treatment is given in Table 2. Four nitrogen rates (0, 50, 100, 150 kg ha^{-1}) were applied to each irrigation treatment. Half nitrogen dose was applied as side dressing with the help of a single row hand drill at the time of planting and remaining half dose was applied with first irrigation. Phosphorus @ 100 kg ha^{-1} was applied to all plots at the time of planting. Urea and triple super phosphate (TSP) were used as a source of fertilizers. The experiments were laid out in randomized complete block design in a split-plot arrangement with irrigation in main plots and nitrogen in sub plots. Every treatment was replicated three times for a total of 48 plots of 1.5 m x 6m (9 m^2). All other cultural practices were standard and uniform for all treatments·

Grain filling rate was determined by taking samples consisting of 5 spikes from a sub-plot, taken twice a week in the beginning and at 7 days interval for last three samples. Sampling was started 7days after anthesis. Central portion from each spike was cut, dried at 80°c up to a constant weight, and then recorded the grain dry weight after thrashing. Grain filling rate (g day$^{-1)}$ was calculated as the increase in grain dry weight in a unit of time whereas grain filling duration (days) was taken as the number of days from anthesis to the day of physiological maturity.

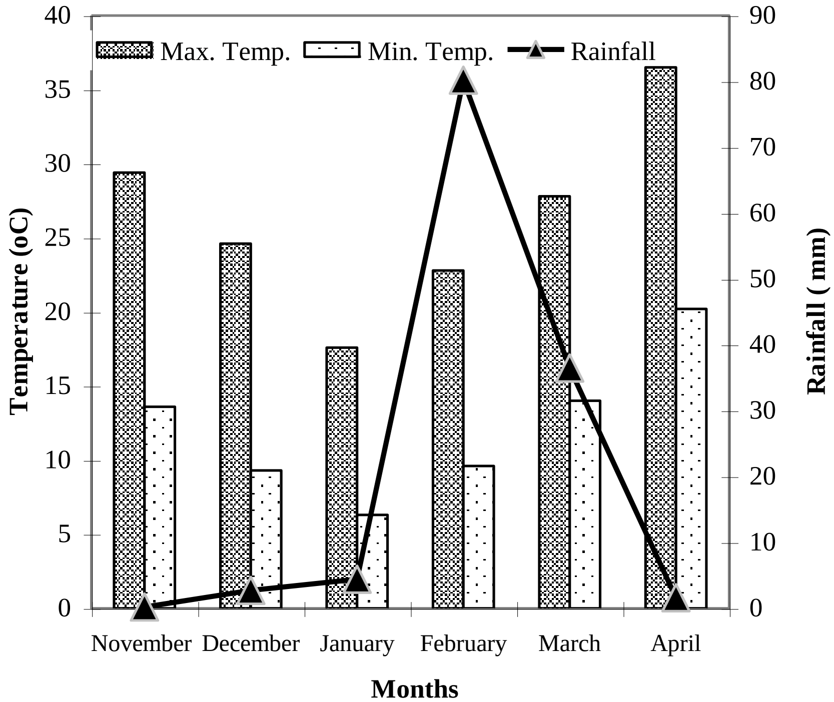

Fig. 1. Meteorological data for the year 2002-03.

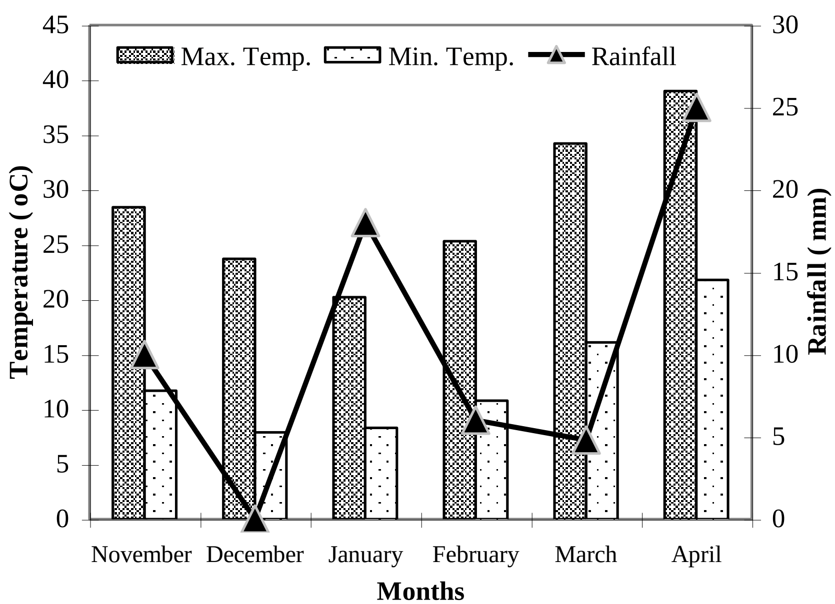

Fig. 2. Meteorological data for the year 2003-04.

Table 1. Soil Characteristics of experimental site.

Characteristic	Results	
	2002-03	2003-04
PH	8.01	8.10
Electrical conductivity (dS m^{-1})	1.51	1.59
Total soluble salts (%)	0.10	0.10
CO_3 (me L^{-1})	Nil	Nil
HCO_3 (me L^{-1})	4.1	5.5
CI (me L^{-1})	7.7	7.5
SO_4 (me L^{-1})	3.3	3.3
Ca + Mg (me L^{-})	7.65	6.4
OM (%)	0.60	0.73
Available P (ppm)	5.6	5.0
Available K (ppm)	161	175
Total N (%)	0.031	0.037
Texture	Sandy loam	Sandy loam

Table 2. Grain yield and its components of spring wheat under different levels of irrigation and nitrogen in the year 2002-03.

Treatments	Grain yield (kg ha^{-1})	1000-grain weight (g)	Spike length (cm)	Spikelets $spike^{-1}$	No. of grains $spike^{-1}$	Spike m^{-2}	Harvest index (%)
Irrigations							
I_1	3208.25 d	42.01 d	9.93 c	16.72 b	43 c	570.25 b	33.00 c
I_2	3527.75 c	42.66 c	10.66 b	17.03 b	48 b	537.42 b	34.00 bc
I_3	3952.83 b	43.31 b	10.91 ab	17.29 ab	51 ab	568.00 b	35.00 ab
I_4	4729.25 a	44.04 a	11.35 a	17.78 a	55 a	714.67 a	36.00 a
Nitrogen							
N_0	3093.75 d	42.01 b	9.24 c	15.75 b	39 d	503.42 c	32.00 b
N_1	3619.58 c	42.86 ab	10.61 b	17.05 a	47 c	564.08 b	34.00 b
N_2	4156.25 b	43.29 a	11.20 ab	17.74 a	53 b	643.42 a	35.00 a
N_3	4548.50 a	43.60 a	11.80 a	18.29 a	57 a	679.42 a	37.00 a
Interaction							
IxN	NS	NS	NS	NS	NS	NS	NS

Data within columns followed by different letters are significantly different at $p<0.05$.

Table 3. Grain yield and its components of spring wheat under different levels of irrigation and nitrogen in the year 2003-04.

Treatments	Grain yield (kg ha^{-1})	1000-grain weight (g)	Spike length (cm)	Spikelets $spike^{-1}$	No. of grains $spike^{-1}$	Spike m^{-2}	Harvest index (%)
Irrigations							
I_1	2970.68 d	40.12 c	9.44 c	13.75 c	33 d	465.50 d	44.00 a
I_2	3664.13 c	40.74 bc	10.50 b	15.75 b	40 c	525.75 c	39.00 b
I_3	5461.34 b	42.00 b	10.76 ab	16.75 b	49 b	587.50 b	39.00 b
I_4	5672.58a	45.50 a	11.36 a	18.75 a	60 a	687.00 a	36.00 c
Nitrogen							
N_0	3939.54 d	41.25 b	9.07 d	15.25 b	43 c	488.75 d	38.00 c
N_1	4293.49 c	42.12 ab	10.15 c	16.50 a	46 bc	520.25 c	39.00 bc
N_2	4546.93 b	42.25 ab	11.13 b	16.50 a	47 ab	594.25 b	40.00 ab
N_3	4988.76 a	42.75 a	11.71 a	16.75 a	50 a	662.50 a	42.00 a
Interaction							
IxN	NS	NS	NS	NS	NS	NS	NS

Data within columns followed by different letters are significantly different at $p<0.05$.

At maturity, one meter square area selected randomly from each plot was used to determine the number of spikes per unit area. Ten spikes from each plot were randomly sampled, threshed manually for the measurement of grains per spike and grain weight. An area of 6 m^2 (4 rows) in both years was harvested manually from the center of each plot for the measurement of grain yield. To avoid border effect 0.5 m of every side in each plot was not considered when harvesting. Harvest index was calculated as the average grain yield per plot divided by the average dry biomass per plot. Data collected during this study were statistically analyzed using MSTAT statistical package of Michigan State University, USA (Anon., 1989). The Duncan's new Multiple Range (DMR) test at 5% probability level was used to test the differences among mean values (Steel & Torrie, 1984).

Results

Grain filling rate: The differences in GFR between irrigation levels were significant ($p \leq 0.01$) at all the harvesting dates (Fig. 3). In both the years, GFR at all irrigation levels increased with increasing number of days after anthesis up to 20 days. After that the GFR showed a decreasing trend at all irrigation levels. The maximum values (0.40 g day^{-1} in 2002-03 and 0.41 g day^{-1} in 2003-04) of grain filling rate were observed in one irrigation treatment at 20 days after anthesis whereas the minimum values of GFR were recorded for four irrigation treatment at all harvest times.

Nitrogen application during both years significantly ($p \leq 0.01$) affected GFR at all harvest times (Fig. 3). The trend in GFR with increasing number of days after anthesis and nitrogen levels was same as observed for irrigation treatments. The maximum GFR of 0.41 g day^{-1} in both years was recorded at 20 days after anthesis, under the nitrogen treatment 0 kg N ha^{-1} followed by 50, 100 and 150 kg N ha^{-1}. The interactions between irrigation and nitrogen (I x N) for GFR were significant only for two initial harvests in 2002-03 and second harvest in 2003-04. For all other harvests the I x N interaction was found non significant for both years.

Grain filling duration: Grain filling duration (Fig. 4a and b) showed significant ($p \leq 0.01$) effects of irrigation treatments on GFD of wheat in the year 2002-03 only. During this year the maximum grain filling duration (53 days) was recorded under the treatment where four irrigations (irrigation at tillering, stem elongation, anthesis and grain development) were applied, which was statistically similar to GFD (50.75 days) recorded at three (irrigation at tillering, anthesis and grain development). The minimum GFD (48 days) was recorded under the treatment where only one irrigation was applied at tillering. The effect of nitrogen application and the interactions between nitrogen and irrigation on GFD for both the year were non significant.

Grain yield and yield components: Grain yields response varied with the season and yield was higher in 2002-03 seasons than 2003-04. In general, grain yield reduced in each season by decreasing number of irrigations at all nitrogen rates. In both seasons, the average mean grain yield for four, three and two irrigation treatments were 1.68, 1.53 and 1.16 times, respectively, of that for one irrigation treatment. The highest yields of 4548.50 and 4988.76 kg ha^{-1} in 2002-03 and 2003-04 growing seasons, respectively, were recorded for 150 kg N ha^{-1} rate. The average increase in grain yield for both seasons was 38, 25 and 13% at high (150 kg N ha^{-1}), moderate (100 kg N ha^{-1}) and low (50 kg N ha^{-1}) nitrogen levels compared with 0 kg N ha^{-1} treatment. However, the interactive effect of irrigation and nitrogen on grain yield were non significant.

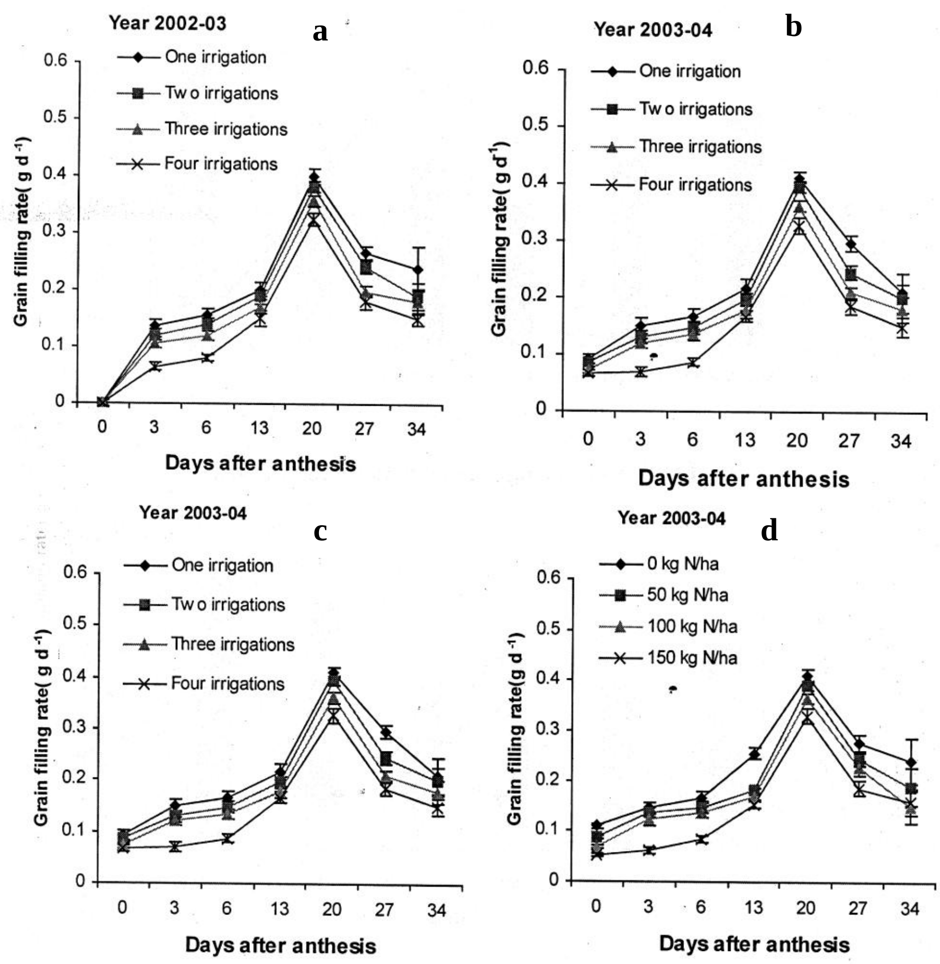

Fig. 3. Effect of different levels of irrigation (a, b) and nitrogen (c, d) on grain filling rate of wheat.

Different irrigation and nitrogen treatments significantly affected the yield components in both years (Tables 2 and 3). In both years, response of all yield components studied was more obvious at four irrigation treatments at all nitrogen rates than all other irrigation treatments. Number of spikes m^{-2} and grains $spike^{-1}$ were affected more by irrigation and nitrogen than grain weight, spike length and spikelets $spike^{-1}$. In both years, the average reductions in spikes m^{-2} and grains $spike^{-1}$ in one irrigation treatment at all N levels were 24% and 36%, respectively.

The harvest index (HI) values varied from 33 to 36% in 2002-03 and 36 to 44% in 2003-04 among different irrigation treatments. Mean harvest index in 2003-04 in plots receiving one irrigation was 22% higher than plots receiving four irrigations. Nitrogen application improved HI in both years with maximum values of 37 and 42% observed with 150 kg ha^{-1} in 2002-03 and 2003-03, respectively.

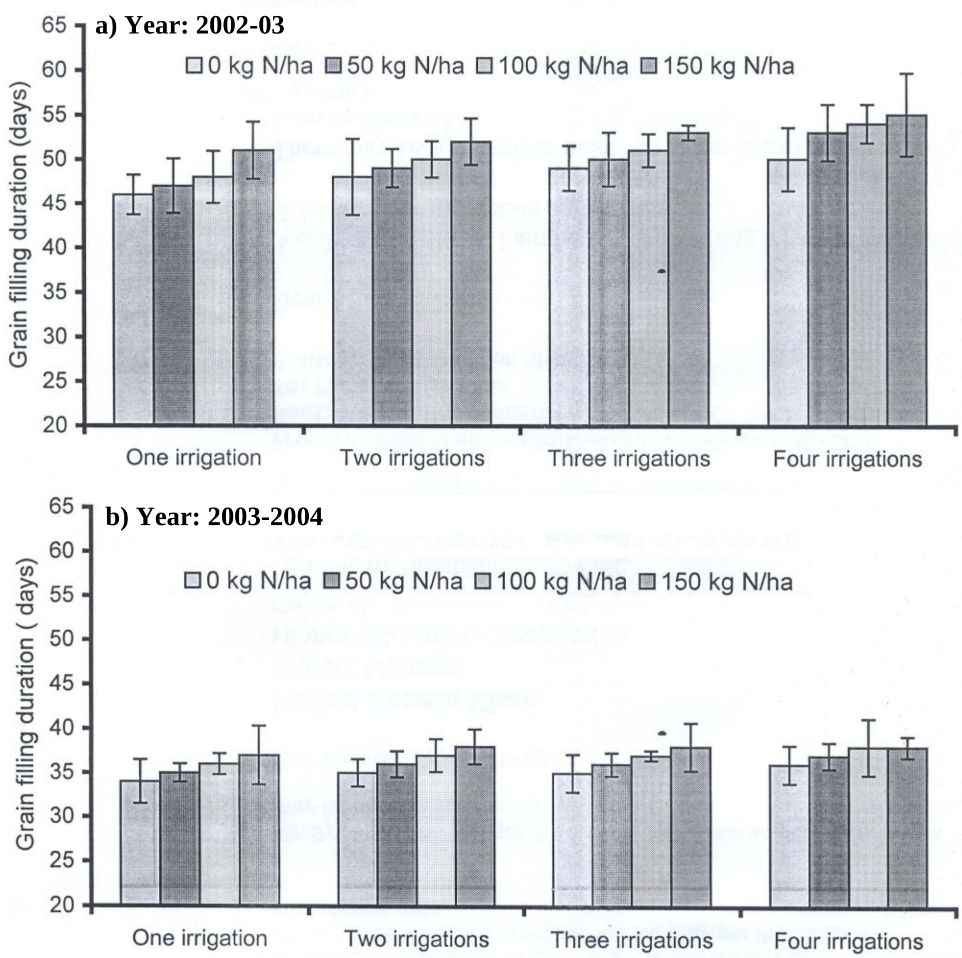

Fig. 4. Effect of different levels of irrigation and nitrogen on grain filling duration of wheat during 2002-03 (a), 2003-4 (b).

Discussion

Grain filling rate in present study was faster in plots receiving less number of irrigations than plots receiving more number of irrigations which is in conformity to the finding of earlier researchers (Zhang *et al*., 1998;Yang *et al*., 2000). Grain filling rate in wheat is regulated by the current supply of photosynthates as well as remobilization of assimilates produced during vegetative stage. Post-anthesis soil drying results in accelerated leaf senescence (Thomas & Stoddart, 1980; Gan & Amasino, 1999) which reduces current supply of assimilates to the grains. Faster GFR in this situation is most probably the result of plants adjustments (escape) to the prevailing water deficit conditions. Accelerated grain filling and increased harvest index under post-anthesis soil drying conditions have also been reported by Zhang *et al*., (1998) and Yang *et al*., (2000) which can be attributed to the remobilization and transfer of the stored assimilates in vegetative tissue to the grain with the initiation of plant senescence (Gan & Amasino, 1997; Nooden *et al*., 1997).

The results are quite in agreement with the findings that remobilization of assimilates to grains, the increase in harvest index under stress is the possible effect of remobilization and transfer of the stored assimilates in vegetative tissue to the grain with the initiation of plant senescence (Gan & Amasino, 1997; Nooden *et al*., 1997). Normally pre-anthesis assimilate reserves in the stem and sheath of wheat contribute 25-33% of the final grain weight (Rawson & Evans, 1971; Gallagher *et al*., 1976; Gebbing & Schnyder, 1999). However, remobilization of reserves to grain is critical to grain yield if the plants are subjected to water stress during grain filling (Nicolas *et al.*, 1985; Palta *et al*., 1994; Ehdaie & Waines, 1996; because early senescence caused by post- anthesis water deficit reduces photosynthesis, shortens the grain filling duration and finally results in reduction of grain weight (Bidinger *et al*., 1977; Brown *et al*., 1991; Palta *et al*., 1994; Zhang *et al*., 1998).

The length of grain filling period (GFD) an important determinant of yield of all grain crops, is also very sensitive to water stress (Egli, 1998) as water stress during grain development shortens the supply of assimilates to developing grains. Nitrogen availability at this time can help plant in increasing GFD by delaying senescence to some extant (Yang *et al*., 2000). The nitrogen application delayed grain filling duration in present study, which may be the result of delayed senescence due to better availability of nitrogen under increased levels of nitrogen. These results are also supported by many earlier reports in literature where researchers reported prolonged GFD with nitrogen application (Hayati *et al*., 1995; Meckel *et al*., 1984; Smiciklas *et al*., 1989; Fredrick *et al*., 1991).

Grain yield in wheat is the result of number of effective tillers, number of grains per spike and grain weight (Ahmad *et al*., 1988). Assimilation and partitioning of photosynthates in relation to grain growth are therefore of vital importance. Responses to irrigation vary among the yield components because of the differences in soil water conditions during the growing season (Frederic & Camberato, 1995b). Irrigation from the beginning of tillering to anthesis in this study resulted in the production of more number of effective spikes and higher grain yield. Matsunaka *et al*., (1992) also reported increased grain yield of wheat with the increase in number of effective spikes per unit area. Increase in grain yield with increasing frequency of irrigation have also been reported by Rai & Sinha (1992); Pratibha *et al*., 1992; Patel & Upadhyay (1993); Frizzone *et al*., (1996); Karim *et al*., (1997) and Gill & Singh (1999).

Nitrogen application is an important input for wheat production. In the present study increasing levels of nitrogen fertilizer improved grain yield, which seems to be the result of enhanced tiller production and increased kernel number per spike. Similar results have also been reported by some other researches (Fredrick & Camberato, 1995b). The possible reason of increased grain yield with adequate nitrogen supply may be the result of delayed leaf senescence, sustained leaf photosynthesis during the grain filling period and extended duration of grain fill (Fredrick & Camberato, 1995b).

On the basis of the results of this study it is concluded that decreasing number of irrigation accelerated the GFR and hastened the GFD, whereas N application increased GFR and Duration at all irrigation levels. Reduction in grain yield under less irrigation treatment is the result of a significant reduction in number of effective tillers and nitrogen supply improved effective tillers per unit area at all irrigation levels.

Reference

Ahmad, N., S.M.A. Basra, R.H. Qureshi and S. Ahmad. 1988. Grain development in wheat as affected by different nitrogen levels under warm dry conditions. *Pak. J. Agri. Sci*., 25: 225-231.

Anonymous. 1954. *U.S. Salinity Lab. Staff, Diagnosis and improvement of saline alkaline soil. USDA Hand Book No*. 60, Washington, D.C., pp. 160.

Anonymous. 1986. MSTAT Micro-Computer Statistical Programme. Michigan State. East Lansing, Michigan, USA.

Bidinger, F., R.B. Musgrave and R.A. Fischer. 1977. Contribution of stored pre-anthesis assimilate to grain yield in wheat and barely. *Nature*, 270: 431-433.

Brown, J.H., G. Pliyath and J.E. Thompson. 1991. *Plant Physiology: Physiological mechanisms of plant senescence*, a Treatise, Growth and Development: (Ed): F.C. Steward. Academic Press, New York, pp. 227-275.

Egli, D.B. 1998. Variation in leaf starch and sink limitations during seed filling in soybean. *Crop Sci*., 39: 1361-1368.

Ehdaie, B. and J.G. Waines. 1996. Genetic variation for contribution of pre-anthesis assimilates to grain yield in spring wheat. *J. Genetics Breeding*, 50: 47-55.

Frederick, J.R. and J.J. Camberato. 1994. Water and nitrogen effects on winter wheat in Southern Coastal Plain: Physiological responses. *Agron. J*., 87: 527-533.

Frederick, J.R. and J.J. Camberato. 1995b. Water and nitrogen effects on winter wheat in the southeastern coastal plain: II- Physiological responses. *Agron. J*., 4: 241-248.

Frederick, J.R., J.T. Wooley, J.D. Hesketh and D.B. Peters. 1991. Seed yield and agronomic traits of old and modern soybean cultivars under irrigation and soil water deficit. *Field Crops Res*., 27: 71-82.

Frizzone, J.A., A.V. Mello, M.V. Folegatti and T.A. Botrel. 1996. Different water depth and nitrogen fertilization effect on wheat crop yield. *Pesquisa Agropecuaria Brasileira*, 31: 425-434.

Gallagher, J.N., P.V. Biscoe and B. Hunter. 1976. Effects of drought on grain growth. *Nature*, 264: 541-542.

Gan, S. and R.M. Amasino. 1997. Making sense of senescence: molecular genetic regulation and manipulation of leaf senescence. *Plant Physiol*., 113: 313-319.

Gebbing, T. and H. Schnyder. 1999. Pre-anthesis reserve utilization for protein and carbohydrate synthesis in grain of what. *Plant Physiol*, 121: 871-878.

Gill, M.S. and K. Singh.1999. Effect of irrigation regimes, rates of nitrogen on yield and quality of durum wheat. *J. Agronomic Res*., 36: 180-186.

Hayati, R., D.B. Egli and S.J. Crafts-Brandner. 1995. Carbon and nitrogen supply during seed filling and leaf senescence in soybean. *Crop Sci*., 35: 1063-1069.

Karim, A.J.M.S., K. Egashira and M.J. Abedin. 1997. Interaction effects of irrigation and nitrogen fertilization on yield and water use of wheat, grown in a clay terrace soil in Bangladesh. *Bull. Inst. Tropical Agri., Kyushu Univ*., 20: 17-26.

Li, A.G., Y.S. Hou, G.W. Wall, A. Trent, B.A. Kimbal and P.J. Pinter. 2000. Free air carbon dioxide enrichment and drought stress effects on grain filling rate and grain filling duration in spring wheat. *Crop Sci*., 40: 1263-1270.

Matsunaka, T., H. Takeuchi and T. Miyawaki. 1992. Optimum irrigation period for grain production in spring wheat. *Soil and Plant Nutrition*, 38: 269-279.

Meckel, I., D.B. Egli, R.E. Phillips, D. Radeliffe and J.F. Leggett. 1984. Effect of moisture stress on seed growth in soybean. *Agron. J*., 75: 1027-1031.

Moodie, C.D., H.W. Smith and P.R. McCreery. 1959. *Laboratory manual of soil fertility*. Staff College of Washington, D.C. USA, pp. 175.

Nicolas, M.E., H. Lambers, R.J. Simpson and M.J. Dalling. 1985. Effect of drought on metabolism on partitioning of carbon in two wheat varieties differing in drought tolerance. *Ann. Bot*., 55: 727-747.

Nooden, L.D., J.J. Guiamet and I. John. 1997. Senescence mechanisms. *Physiol. Plant*., 101: 746-753.

Palta, J.A., T. Kobata, N.C. Turner and I.R. Fillery. 1994. Remobilization of carbon and nitrogen in wheat as influenced by post-anthesis water deficits. *Crop Sci*., 34: 118-124.

Patel, R.M. and P.N. Upadhyay. 1993. Response of wheat (*Triticum aestivum* L.) to irrigation under varying levels of nitrogen and phosphorus. *Ind. J. Agron*., 38: 113-115.

Pratibha, G., N.V. Ramaiah and V. Satyanarayana. 1992. Response of wheat varieties to irrigation schedule. *Ind. J. Agron*., 37: 575-576.

Rai, R. and M.N. Sinha. 1992. Limited water supply for late sown wheat under two NP levels. *Ann. Agri*. *Res*., 13: 419-420.

Rawson, H.M. and L.T. Evans. 1971. The contribution of stem reserves to grain development in a range of wheat cultivars of different height. *Aust. J. Agric. Res*., 22: 851-863.

Singh, U. and P.W. Wilkens. 1999. Simulating water and nutrient stress effects on phenological development in maize. *Field Crop Res*., 44: 1-5.

Smiciklas, K.D., R.E. Mullen, R.E. Carlson and A.D. Knapp. 1989. Drought induced stress effect on soybean seed calcium and quality. *Crop Sci*., 29: 1519-1523.

Steel, R.G.D. and J.H. Torrie. 1984. *Principles and Procedures of Statistics: A Biometrical Approach*. 2nd Ed., McGraw Hill Book Co. Inc., Singapore. pp. 172-177.

Thomas, H. and J.L. Stoddart. 1980. Leaf senescence. *Annu. Rev. Plant Physiol*., 31: 83-111.

Watanabe, F.S. and S.R. Olsen. 1965. Test of an ascorbic acid method for determining P in water and bicarbonate extracts from soil. *Siol. Sci. Soc. American Proc*., 29: 677-678.

Westage, M.E. 1994. Water status and development of maize endosperm and embryo during drought. *Crop Sci*., 34: 76-83.

Yang, J., J. Zhang, Z. Huang, Q. Zhu and L. Wang. 2000. Remobilization of carbon reserves are improved by controlled soil-drying during grain filling of wheat. *Crop Sci*., 40: 1645-1665.

Zhang, H., T. Oweis, S. Garabet and M. Pala. 1998. Water use efficiency and transpiration efficiency of wheat under rainfed and irrigation conditions in Mediterranean environment. *Plant Soil*., 201: 295-305.

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