Effect of Water Deficit on Accumulation of Dry Matter, Carbon and Nitrogen in the Kernel of Wheat Genotypes Differing in Yield Stability

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Water stress effects on accumulation of dry matter, carbon and nitrogen in grains were analysed in varieties and species of wheat differing in yield stability. Variable water environments were generated using a line source sprinkler system. Although large fluctuations occurred in the water potentials of the flag leaf and ear, grain growth remained relatively buffered under moisture stress. Developing grains were at a lower moisture level throughout grain growth in plants subjected to moisture stress relative to the unstressed plants. Carbon content decreased more than the nitrogen content in the stressed grains of the species and varieties. Reduction in the duration of grain growth and the rate of dry weight accumulation induced by water stress was more prominent in *T. aestivum* var. C306 and *T. sphaerococcum*. Grain yield was reduced significantly under water stress, the maximum being in the high yielding cultivar HD2329. Both grain number and grain weight were reduced in response to stress, the extent of reduction being different in different genotypes.

Key words: Water deficit, yield stability, C and N accumulation, heat degree days.

INTRODUCTION

Breeding for drought tolerance is a major objective in many wheat improvement programmes around the world. Several efforts have been made to develop suitable selection criteria for drought tolerance in wheat (Sinha *et al.*, 1986). In this context, the importance of exploiting genetic diversity existing in the wild and alien species of wheat has often been emphasized (Fedak, 1985).

A major approach to identify drought tolerant genotypes has been to assess drought tolerance on the basis of yield stability or drought susceptibility index (Finlay and Wilkinson, 1963; Sinha *et al.*, 1986). Varieties identified on the basis of stability index are, however, usually average or poor yielders (Fischer and Maurer, 1978; Sinha *et al.*, 1986; Aggarwal *et al.*, 1986; Bruckner and Frohberg, 1987). Therefore, the character of drought tolerance observed in wild species needs to be examined critically to reassess if it is linked to mere survival or whether the wild relatives of *T. aestivum* are in fact endowed with certain physiological, phenological or metabolic attributes which contribute to drought tolerance.

Wheat is grown in the post-rainy season in northern India and its productivity is influenced by the water availability and temperatures during grain development period. Many studies have indicated that water stress occurring during early grain development reduces final grain dry mater (Asana and Saini, 1962; Asana and Basu, 1963; Brocklehurst, 1978). Amongst the yield components, grain weight is more stable than grain number under various environmental conditions (Fischer and Turner, 1978). Varieties differing in grain weight, therefore, provide important genetic material for understanding the effects of water stress on processes leading to the ultimate size of the grain. A wealth of information exists on water relations, metabolism and development of individual grains as affected by water availability and temperatures under controlled conditions (Passioura, 1976; Barlow *et al.*, 1980; Sofield *et al.*, 1977; Jenner, Ugalde and Aspinall, 1991). Such information is valuable in understanding the mechanism of individual stress responses. Nevertheless in nature, especially under tropical conditions, both water and high temperature stresses occur together and the resulting field scenario is much more complex.

In view of the above facts, the present study was undertaken to examine the water stress effects on grain growth, carbon and nitrogen accumulation in grains of varieties and species of field grown wheat differing in yield stability. In this paper the approach of expressing the results on the basis of accumulated degree days has been adopted. Grain growth of wheat can be expressed as a function of accumulated heat degree days (Saini and Dadhwal, 1986). This expression helps in comparing water stress effects on varieties and species which due to difference in phenology underwent grain development at different ambient temperatures. This approach, which certainly facilitates the comparison of results obtained in various geographic locations endowed with different environmental conditions, has been used by a few others (Spiertz, 1977; Cerning and Guilbot, 1971).

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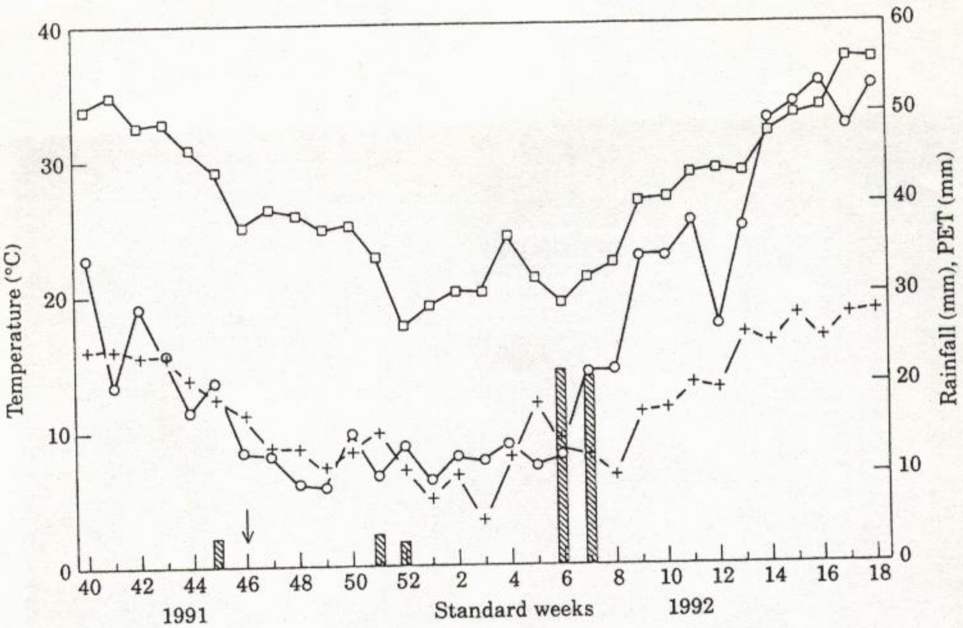

FIG. 1. Weekly meteorological data from October to April of 1991–92. First week of October is 40. ↓ indicates the week of sowing. Max. temp. (□–□), min. temp. (+–+), rainfall (■) and potential evapotranspiration (PET) (○–○).

MATERIAL AND METHODS

The varieties and species chosen for study included two varieties of *T. aestivum* (6*x*), HD2329 and C306 and two species namely *T. sphaerococcum* (4*x*) and *T. polonicum* (6*x*) which have earlier shown contrasting behaviour in terms of stability in grain yield in stress environments (Sinha *et al.*, 1986; Bansal and Sinha, 1991). Cultivar C306 and *T. sphaerococcum* have shown greater stability in grain yield under water limited environments (Sinha *et al.*, 1986; Bansal and Sinha, 1991) than HD 2329 and *T. polonicum* respectively. These genotypes were raised during winter season (Nov.–Apr.) in 1991–92 at the research farm of the Indian Agricultural Research Institute, New Delhi, India.

There were four replications and the experimental design was split-plot with variety as the main plot and irrigation as sub-plot. The main plot size was $2{\cdot}5 \times 12{\cdot}5$ m with a row spacing of 25 cm. Each main plot was delimited lengthwise into four sub-plots of 3 m each. The sub-plots represented different water regimes. Seed rate was 100 kg ha^{-1}. Nitrogen, phosphorus and potash were supplied as urea, single superphosphate and murate of potash at the rate of 60:50:40 kg ha^{-1} at the time of sowing. Soil was sandy loam with a mean depth of 3 m and bulk density of 1·55 g cm^{-3}.

An irrigation of 6 cm was given before sowing. The available soil water content (0–180 cm soil depth) at sowing was 23·3 cm. Subsequently, two irrigations were given at 60 and 140 days after sowing using a line source sprinkler technique creating different water regimes in each plot. The results reported are from the area nearest to the sprinkler (well watered region, T1) and the one farthest from it (severely stressed region, T2), the differences between the plants growing in the two regions being the maximum. Both irrigations cumulatively gave 10·07 cm water in T1 and nil in T2 region. Total rainfall was 5·95 cm during the crop season. Total water availability in well watered (T1) and stressed region (T2) was 39·32 and 29·25 cm respectively. The weekly average of minimum and maximum temperatures and weekly total of potential evapotranspiration (PET) and rainfall are depicted in Fig. 1.

Plant stress was quantified by measuring flag leaf and ear water potentials using a pressure chamber (Soil Moisture Equipments Corp, USA) during grain growth period. The water potentials were measured between 1030 and 1130 h on each sampling day, in three replicates. The middle four whorls of spikelets from uniform mother shoots tagged at anthesis were sampled at weekly intervals after anthesis for monitoring grain growth, grain carbon and nitrogen accumulation. Fifteen ears per replicate were used for determining fresh and dry weights. There were four replicates for each treatment. Total carbon and nitrogen were estimated in oven dried samples using an element analyser (2400 CHN Elemental Analyser, Perkin Elmer). Yield and yield components were recorded at harvest. The land area harvested from each plot was 2 m^2. There were four plots for each treatment.

Accumulated degree days (ADD) were computed using the formula:

$$\text{ADDS} = \Sigma(\text{average base temperature} - \text{base temperature})$$

A base temperature of 5 °C was used (Aggarwal and Penning De Vries, 1989). Data were analysed using analysis of variance (Snedecor and Cochran, 1967).

RESULTS

The crop growth duration was 135, 138, 147 and 160 d and anthesis occurred 97, 103, 114 and 126 d after sowing in HD2329, C306, *T. sphaerococcum* and *T. polonicum* plants

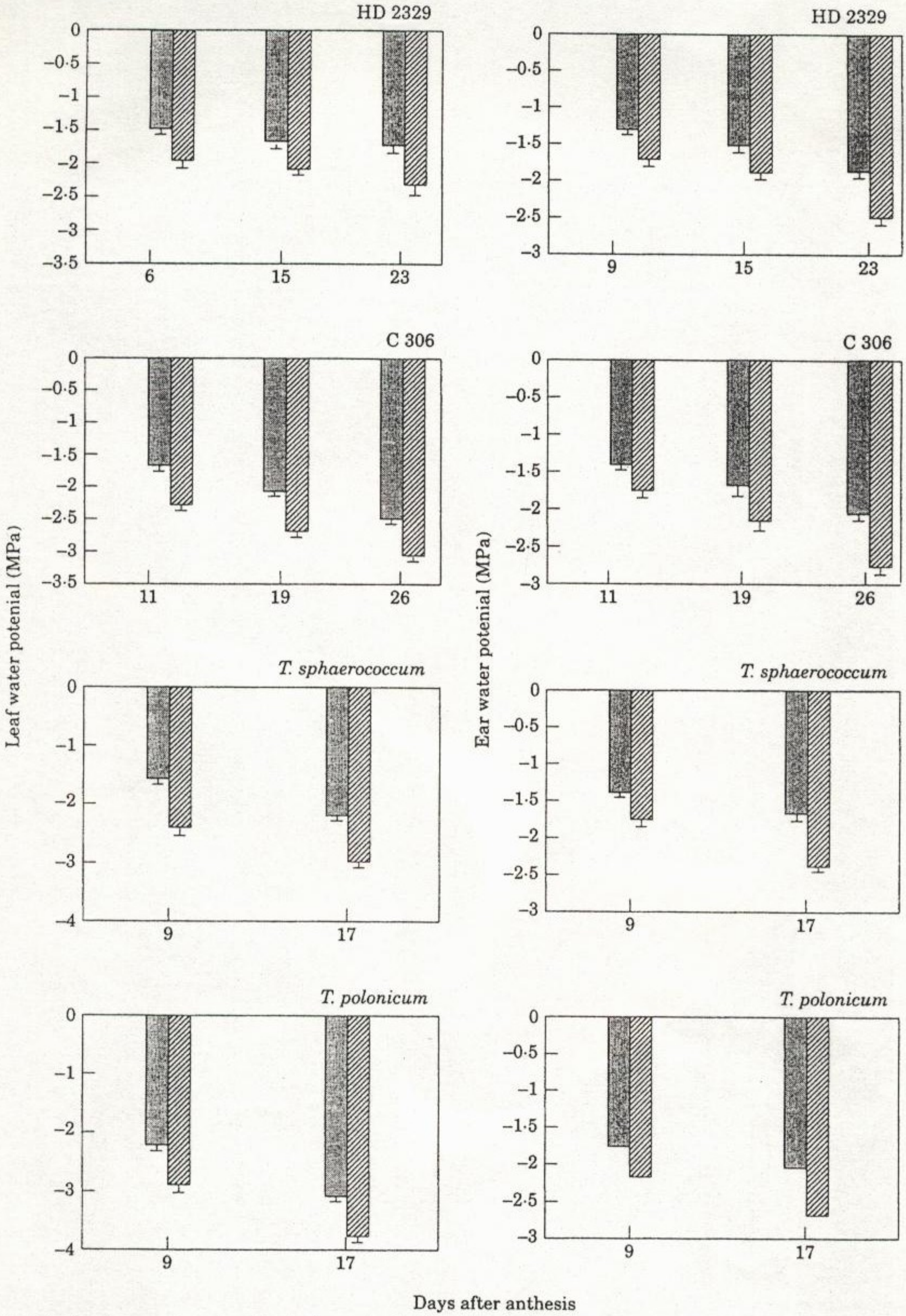

FIG. 2. Changes in leaf and ear water potentials during grain development in wheat varieties and species grown at different levels of water availability. (▨) T1, (▩) T2.

growing in well watered region respectively. The duration of grain filling was 39, 36, 34 and 35 d in HD2329, C306, *T. sphaerococcum* and *T. polonicum* respectively. Water stress reduced grain growth duration (GGD) by 2 d in HD2329 and by 4–5 d in C306, *T. sphaerococcum* and *T. polonicum* respectively. The accumulated degree days required for grain growth were also reduced by 6 % in HD2329 and by 10–13 % in the remaining genotypes.

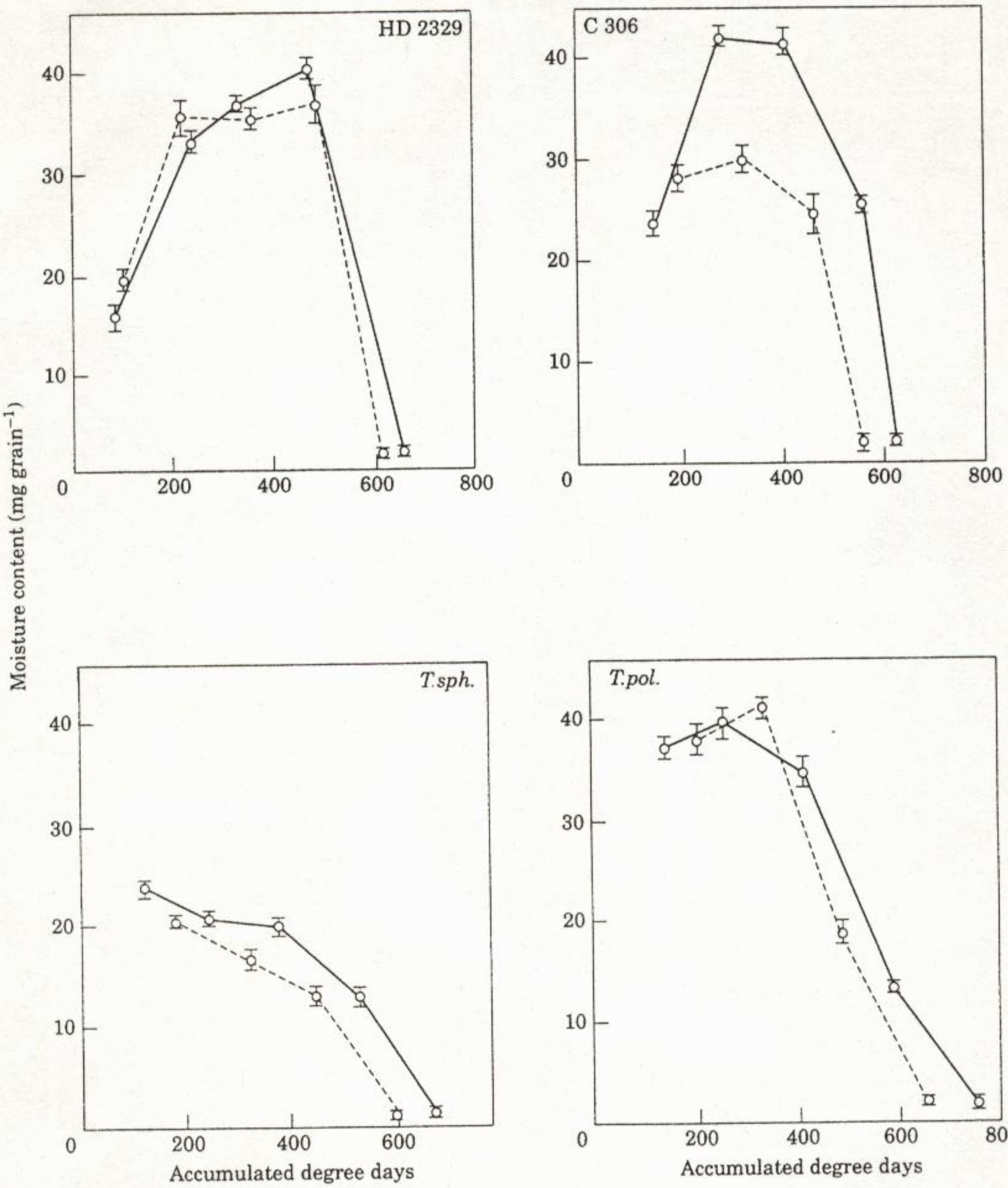

FIG. 3. Grain moisture content in wheat varieties and species grown at different levels of water availability as a function of accumulated heat degree days. T1 (○—○), T2 (○---○).

Flag leaf water potential declined by 0·5–0·8 MPa and ear water potential declined by 0·4–0·7 MPa due to water deficit in the varieties and species during grain filling period (Fig. 2). The moisture content of grains declined rapidly after an initial increase in HD2329 and C306 while in the wild species, a slow declining trend was observed even during early grain growth (Fig. 3). The grain moisture content was lower at different stages of grain growth under stress compared to the respective controls especially in C306 and *T. sphaerococcum*.

Water stress reduced grain weight in middle spikelets of mother shoot in C306 and *T. sphaerococcum* only, the reduction being 25 and 15% relative to the control. Grain weight in water stressed and control plants was similar in HD2329 and *T. polonicum* (Fig. 4). A comparison of average rates of dry matter accumulation during grain growth in the varieties and species showed that stress-induced reduction in the rates of dry matter accumulation was more in C306 and *T. sphaerococcum* compared to the other two (Table 1).

Carbon constituted about 42·5–44·3% of the dry weight at harvest, while nitrogen constituted about 2·2–2·8% in the wheat species and varieties. Moisture stress reduced grain carbon and nitrogen contents relatively more in C306 and *T. sphaerococcum* (Figs 5 and 6). The rate of grain carbon accumulation (mg C per grain per ADD) was similar under control and water stressed conditions in HD2329, while it was reduced in C306, *T. sphaerococcum* and *T. polonicum* under water stress. The average rates of nitrogen accumulation were reduced in all the varieties in water stressed

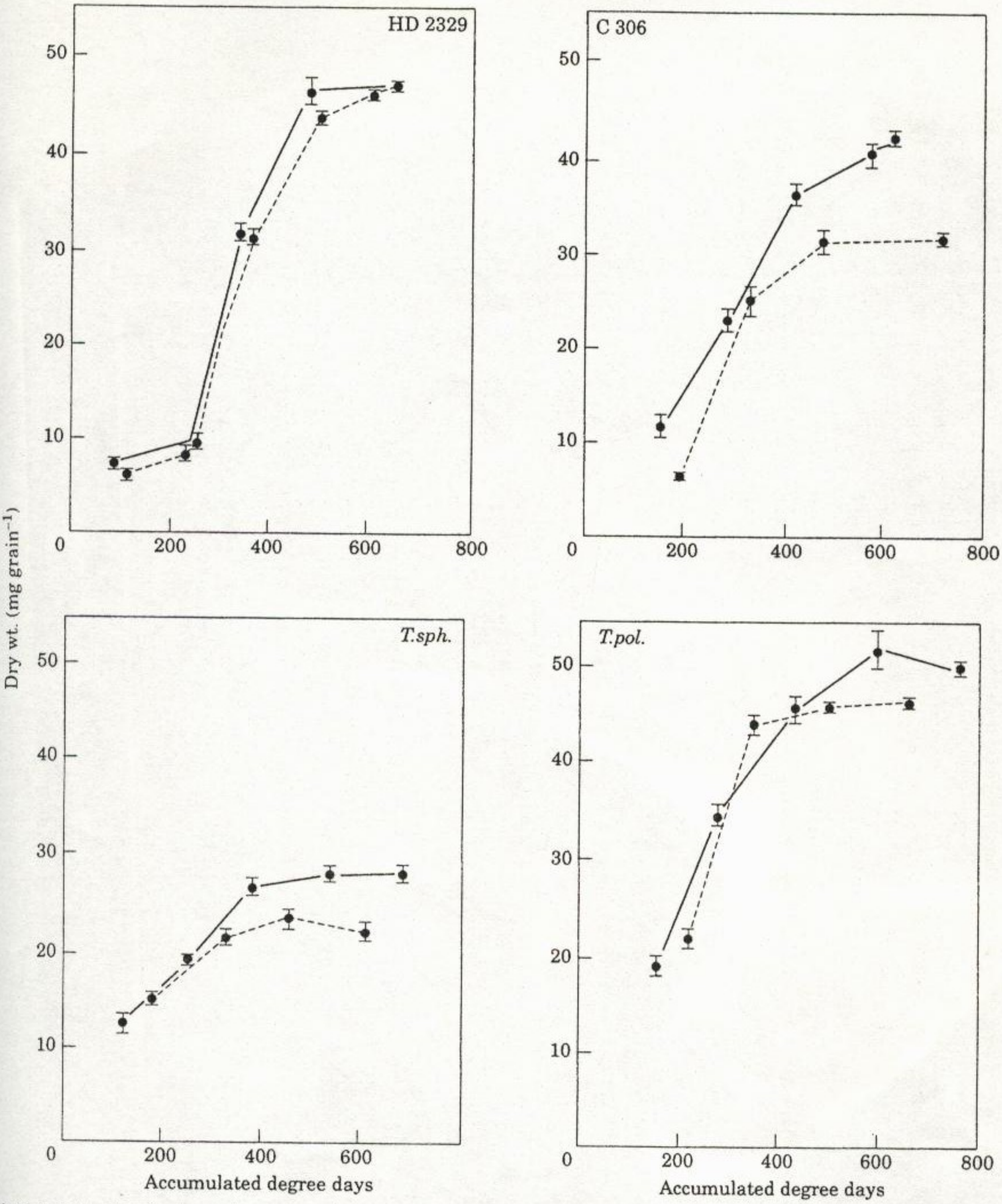

FIG. 4. Grain dry matter in wheat varieties and species grown at different levels of water availability as a function of accumulated heat degree days. T1 (●—●), T2 (●---●).

plants but the reduction was remarkably higher in C306 and *T. sphaerococcum*.

Grain yield was reduced in all varieties and species due to water stress. The reduction in yield was 30% in HD2329, 18% in C306 and *T. polonicum* and 15% in *T. sphaerococcum* respectively (Fig. 7). Both grain number and grain weight were reduced in response to water stress. However, in HD2329 and *T. polonicum* reduction in grain number contributed more toward reduction in grain yield while in C306, grain weight was reduced more than grain number due to moisture stress. In *T. sphaerococcum* both grain number and grain weight (Fig. 7) contributed to the decline in grain yield under stress.

DISCUSSION

Growth of grains collected from middle spikelets of mother shoot was found to remain relatively buffered under drought stress although large fluctuations occurred in the water potentials of the flag leaf and ear. Grain moisture expressed as percent of grain weight declined in all varieties and species during grain development reflecting the deposition

TABLE 1. *Average growth rates of dry matter, carbon and nitrogen accumulation in the grains of well watered and water stressed wheat varieties and species*

Treatment	*T. aestivum* HD2329	*T. aestivum* C306	*T. sphaerococcum*	*T. polonicum*
μg d. wt per grain per ADD				
T1	43·78 ± 0·49	75·28 ± 0·22	46·40 ± 0·53	76·40 ± 0·55
T2	36·78 ± 0·42	51·78 ± 0·32	32·83 ± 0·37	61·90 ± 1·24
μg C per grain per ADD				
T1	30·85 ± 0·11	32·65 ± 0·32	18·70 ± 0·85	33·50 ± 1·41
T2	32·60 ± 0·71	22·40 ± 0·35	16·78 ± 1·49	27·70 ± 0·21
μg N per grain per ADD				
T1	1·73 ± 0·02	1·76 ± 0·01	1·29 ± 0·09	1·76 ± 0·10
T2	1·53 ± 0·75	1·17 ± 0·06	0·95 ± 0·04	1·68 ± 0·01

The values are means of four replicates with 60 grains constituting a replicate. The rates have been calculated during entire period of growth.

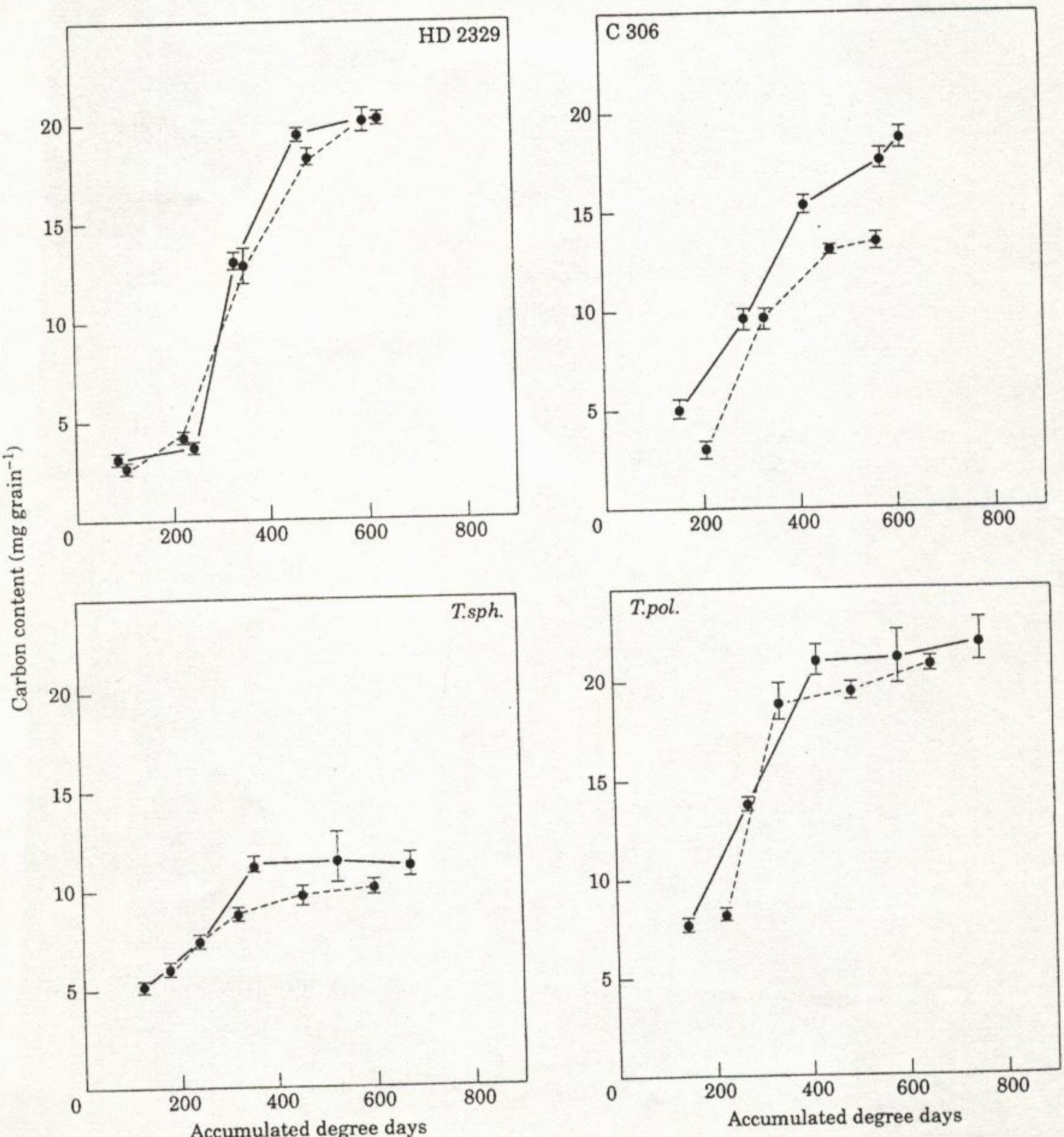

FIG. 5. Grain carbon contents in wheat varieties and species grown at different levels of water availability as a function of accumulated heat degree days. T1 (●—●) and T2 (●---●).

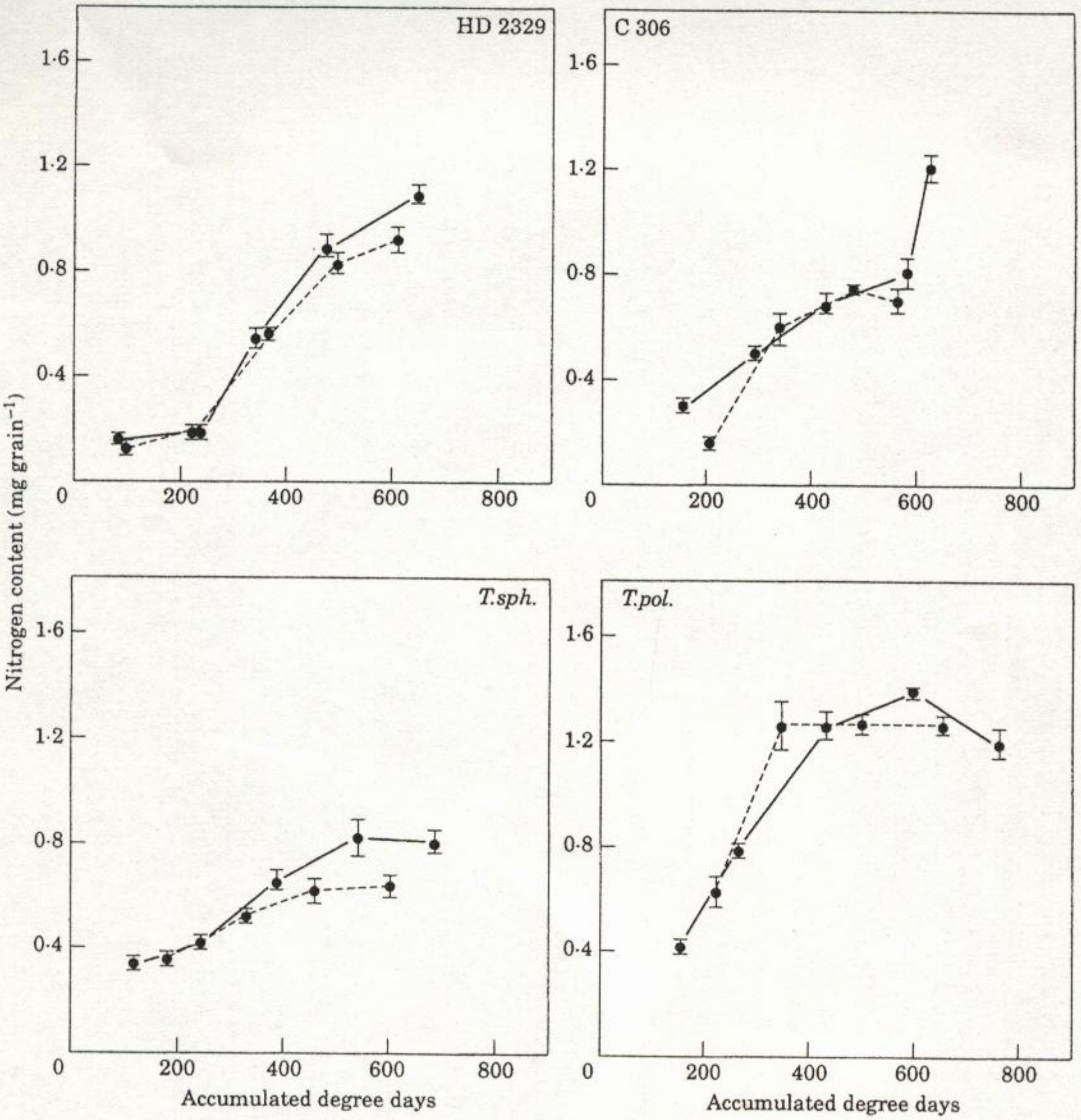

FIG. 6. Grain nitrogen contents in wheat varieties and species grown at different levels of water availability as a function of accumulated heat degree days. T1 (●—●), T2 (●---●).

of starch, protein and other metabolites (Fig. 3, Jenner *et al.*, 1991). The continuous decline in the moisture content of grains in *T. polonicum* especially from 2 weeks after anthesis seemed to be largely due to the higher rates of dry matter accumulation in this species. On the other hand, grains of *T. sphaerococcum* had higher water loss coupled with lower rates of dry matter accumulation. It is generally agreed, that if the deceleration of dry matter accumulation precedes the loss of water, then other factors must have been responsible for the reduction in dry matter accumulation (Sofield *et al.*, 1979). In *T. sphaerococcum*, the first sampling was done 8–10 d after anthesis and the two processes were found to be coupled from then on, suggesting that the possibility of water loss leading to cessation of grain growth cannot be ruled out. Grains of water stressed plants lost water sooner compared to the grains in control plants during development.

The grain carbon and nitrogen accumulation pattern indicated differences in the relative sensitivity of the two processes to water stress (Figs 5 and 6). Carbon content decreased more than the nitrogen content in the stressed grains. Water stress induced higher nitrogen per cent (data not shown) in grains in both the varieties and species. Biochemical processes concerned with protein accumulation have been observed to be more heat tolerant (Bhuller and Jenner, 1985; Tashiro and Wardlaw, 1991) compared to the rate as well as duration of starch synthesis (Gallagher, Biscoe and Hunter, 1976; Tashiro and Wardlaw, 1991). It is also realized generally that while water stress increases the C and N percentage in grains at maturity, the contents per grain might be reduced (Figs 5 and 6, Tashiro and Wardlaw, 1990).

Grain dry weight is an expression of the rate of dry matter accumulation and grain growth duration (Brocklehurst, 1978). Water stress reduced grain dry weight (main shoot) of cv. C306 and *T. sphaerococcum* by reducing both the duration and the rates of dry matter accumulation (Table 1). Cv. C306 and *T. sphaerococcum* also suffered higher

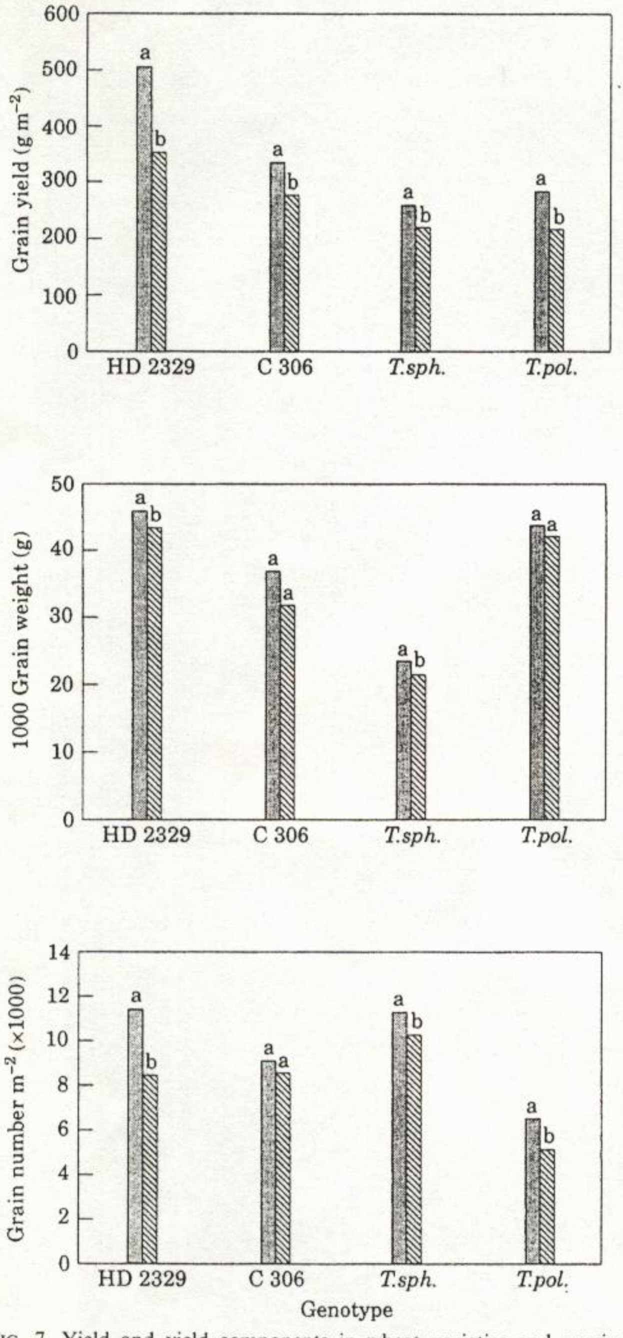

FIG. 7. Yield and yield components in wheat varieties and species grown at different levels of water availability. The Critical Difference at 5% probability for treatment: grain yield (23·26); grain no. (940) and 1000 grain weight (1·77). The letters a and b indicate that the difference between the treatments is significant and 'aa' indicates that the difference is non-significant. (▨) T1, (▧), T2.

reduction in thousand grain weight under stress relative to the control (Fig. 7). Similarly the dry matter accumulation of grains from middle spikelets was also reduced only in C306 and *T. sphaerococcum* under stress. Our results confirm the earlier observations of Aggarwal and Sinha (1984) who had tried to analyse the basis of higher stability in grain yield of wheat cultivars in drought environments. They observed that the cv. C306, which shows higher stability in grain yield in water stress environments relative to the high yielding cultivar Kalyansona, also showed higher reduction in grain weight but maintained grain number. Further, temperature is known to have a profound effect on duration of grain filling also. High temperatures during grain growth will fulfil the requirement of ADDs early and thus the duration of grain development is reduced with adverse effects on yield (Saini and Dadhwal, 1986).

Water deficit resulted in significant reduction in grain yield, the maximum being in the high yielding cultivar, HD2329 (Fig. 7). Water stress reduced both grain numbe and thousand grain weight but the relative contribution c these yield components to reduction in grain yield varied in different varieties and species. Moisture stress-induced reduction in grain yield appeared to be relatively smaller in C306, *T. sphaerococcum* and *T. polonicum* (Fig. 7). The relatively lower yield potential of these varieties and species could itself be one of the reasons for this (Bansal and Sinha, 1991). Further, the extensive canopies of T1 plants in the species of longer duration also lost moisture and even showed slight stress symptoms during later phase of grain filling due to the high PET and temperatures during th period (Fig. 1). Also, plants growing continuously at lower water regime in T2 might have adapted by developing deeper root systems. Stress adaptation in plants is known to manifest through osmotic adjustment, deeper root systems etc. (Morgan, 1984).

Thus, the results of the present investigation indicate that coupling of moisture stress with high temperatures accentuated the effects on grain growth by reducing the grain carbon and nitrogen concentration. Remarkable reduction in C and N contents was observed in the more stable genotypes and was associated well with the reduction in individual grain weight.

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