THE EARLY STAGES OF GRAIN DEVELOPMENT IN WHEAT: RESPONSE TO WATER STRESS IN A SINGLE VARIETY

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Abstract

In wheat (*Triticum aestivum* cv. Gabo) a temporary water deficit in the first 7 days following anthesis significantly reduced the final grain weight per ear. A reduction in seed set in response to stress was associated with an initially greater rate of development of the remaining grains, with an enhanced rate of cell division in the endosperm. Relative turgidity measurements indicated that the stress applied did not significantly reduce grain water content, although the ear structure showed some water loss, and the stem and flag leaf blade were quite severely stressed. The greater desiccation of the leaf and stem in comparison with the ear was reflected in the lower rate of photosynthesis of these organs under stress conditions.

With the reduction in net photosynthesis, both during and subsequent to the period of water deficit, there was a marked reduction in the storage of dry material in the stem of stressed plants, a temporary cessation of tiller development, and an almost complete inhibition of net root growth in dry weight. However, estimates of net photosynthesis by the upper parts of the plant indicated that this was probably in excess of that required for grain growth in the stressed plants. Also, experiments in which additional grains were removed from the ears of stressed plants 10 days after anthesis gave no indication of a substrate limitation to grain growth. Thus the interaction between a temporary water deficit during the early stages of grain development and final grain yield would appear to be an indirect one.

I. INTRODUCTION

Water deficit during grain development results in a consistent, but not fully understood, pattern of response. Senescence from the lower to the upper leaves is accelerated (Asana, Saini, and Ray 1958; Kydrev and Tyankova 1965), with the result that the total supply of photosynthate to the plant is reduced. Reduced storage of excess assimilates in the stem (Asana and Basu 1963) and a change in the pattern of distribution of current assimilates from the lower parts of the plant to the grain (Wardlaw 1967) follow the reduction in net assimilation. These compensatory changes are often adequate to maintain grain growth until the later stages of development (Asana, Saini, and Ray 1958; Konovalov 1959; Asana and Joseph 1964).

Asana, Saini, and Ray (1958) noted that the rapid termination of grain growth in the later stages of development of water-stressed wheat was associated with a rapid yellowing of the ear tissue, and suggested that the final decline in grain growth was the result of a reduced assimilate supply. However, in more recent experiments,

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Asana and Basu (1963) noted a late accumulation of sugar in the stems of stressed plants and concluded that stress had interfered with the transfer of assimilates into the ear. Aspinall (1965) reached a similar conclusion, when he observed that grain growth in water-stressed barley plants was not affected by leaf or floret removal. In many instances water stress has been shown to have no direct effect on the grain, in that the ear structure and individual grains are relatively resistant to desiccation (Konovalov 1959; Aspinall 1965; Wardlaw 1967; Kydrev 1969).

There is a need to clarify the response of cereals to a water deficit at all stages of development, as it is clear that the response to stress may vary with stage of development and type of growth (Iljin 1957; Wardlaw 1967, 1969). Even within the grain there is a marked change in development with time, with an initial period of cell division and expansion, prior to the main period of starch storage. Aspinall (1965) suggested that the reduced yield of barley subjected to a short-term stress soon after anthesis, although not affecting grain dry weight until towards maturity, may have resulted from an effect on cell development in the young stages.

As a sequel to earlier work on the effect of temperature and light intensity on grain development (Wardlaw 1970), the present experiments were initiated to examine more closely the response of wheat to a water deficit during the period of rapid cell division and expansion in the endosperm, and to assess the role of assimilate supply in regulating the immediate and subsequent growth responses within the plant. Grain set is sensitive to water stress at anthesis and shortly after (Asana and Joseph 1964; Wells and Dubetz 1966) as it is to light intensity and temperature (Wardlaw 1970) and interactions between developing grains may be important in response to stresses at this stage.

II. Methods and Materials

(*a*) *Cultural Conditions*

Wheat plants (*Triticum aestivum* cv. Gabo) were grown singly in perlite in 5-in. pots under natural daylight extended to 16 hr by low-intensity incandescent lamps. Air temperatures were controlled at 21°C for 8 hr of the daylight period and at 16°C for the remainder of the 24-hr cycle. All plants were supplied with standard nutrient solution in the morning and with water each afternoon. Tillers were removed 5 weeks after sowing, and again at anthesis, to allow ease of handling and to give uniformity in leaf area per plant.

At anthesis all plants were transferred to an artificially lit (L.B.H.) cabinet (Morse and Evans 1962). Day length was maintained at 16 hr with VHO daylight fluorescent tubes, supplemented with incandescent lamps. The light intensity measured with a flat EEL selenium photoelectric light-meter was 3500 f.c. Air temperature was held at 21°C and relative humidity at either 45 or 70%. Water stress was obtained by cessation of watering, and allowing the plants to dry out for a period of 6 or 7 days following anthesis.

(*b*) *Photosynthetic Measurements*

Carbon dioxide exchange by the flag leaf blade, ear, and peduncle (top internode immediately below the ear) was examined by enclosing the part, still attached to the plant, in a Perspex chamber 2·0 by 5·0 cm in cross-section. The differential in CO_2 concentration of an air stream before and after passing over the organ was determined with a Grubb–Parsons infrared gas analyser (model SB2) calibrated with Wösthoff gas-mixing pumps. Air flow rates were such that the maximum difference in CO_2 concentration was no greater than 30 p.p.m. by volume and ranged from 1 to 2 litres $min,^{-1}$. All photosynthetic measurements were made in an artificially lit (L.B.H.) cabinet at 3500 f.c. (100 W m^{-2} visible radiation).

(c) *Relative Turgidity*

Relative turgidity was estimated, as in earlier experiments with wheat (Wardlaw 1967), by standing the basal 5 mm of the plant part in water and enclosing the whole in a water-saturated atmosphere. Light intensity was 10 f.c. and temperature 24°C throughout the 5-hr uptake period. Individual wheat grains were placed in water to about one-quarter their depth in a Petri dish. Relative turgidity was calculated as

$$100 \times \frac{\text{initial fresh weight} - \text{oven dry weight}}{\text{saturated weight} - \text{oven dry weight}}.$$

(d) *Endosperm Cell Counts*

The number of cells in the endosperm tissue of a grain was determined using the method described by Rijven and Wardlaw (1966). The endosperm tissue was dissected from the grain, stained with Feulgen's reagent, and macerated by fungal cellulase. The stained nuclei were then precipitated from an aliquot of the resulting suspension and counted under a microscope.

(e) *Experimental Details*

In the first of two major experiments, in which water was withheld from groups of plants from the time of anthesis, plants were rewatered 7 days after anthesis when the flag leaves were severely wilted. Harvests of 10 replicates per treatment were made at anthesis and 8, 16, 24, and 48 days after anthesis for dry weight determination. To assess possible competition between grains for the available supply of assimilates, total grain number was reduced by removing grains from the second lowest florets of all spikelets of both stressed and control plants 10 days after anthesis. In conjunction with the dry weight analyses, further plants were selected for periodic measurement of CO_2 exchange and also for determination of endosperm cell number 8 days after anthesis.

In the second experiment water was withheld until 6 days after anthesis, when wilting was severe, and some plants were sampled at this stage for measurement of relative turgidity in the various organs. Dry weight determinations were made on 12 replicates at anthesis and either 10 or 35 days after anthesis.

The results of these two experiments were complementary, and to simplify the presentation of the data the results from the first experiment have been presented largely in graphical form and full details of the dry-weight responses and error terms have only been tabled for the second experiment.

A supplementary experiment was included to give more information on the changes in photosynthesis of the ear, stem, and leaf, in relation to relative turgidity, as the plants entered stress.

III. Results

In the first experiment there was initially a small, but statistically significant, increase in grain weight per ear of stressed plants by 8 days after anthesis (Fig. 1), despite a reduction in mean number of grains set from 41 to 36 per ear (see legend to Fig. 5). Up to 24 days after anthesis there was little difference in grain weight per ear between stressed and control plants, but subsequently there was more growth by the control grains, resulting in a significantly higher grain weight in control ears at maturity (48 days after anthesis). Dry weight accumulation was depressed in both the stem and roots of stressed plants, with a very marked effect on the root system.

In Figure 2 the top two internodes have been examined separately. The top internode, which was still increasing in dry weight and height immediately after anthesis, was much less sensitive to water stress than the next internode below, which was a storage organ at this stage (Wardlaw and Porter 1967).

In addition to the organs already discussed the regrowth of tillers was extremely sensitive to water deficit. Eight days after anthesis the 10·2 tillers on control plants weighed 309 mg, while the 3·9 tillers on stressed plants weighed only 21 mg.

Water stress severely reduced net photosynthesis of the flag leaf blade, top internode, and ear (Fig. 3, day 7). However, in the ear and to a lesser extent in the stem dark respiration is large in relation to photosynthesis and net photosynthesis does not necessarily reflect the effect of water stress on the photosynthetic activity of a particular organ. From 16 to 24 days after anthesis, in plants with adequate moisture, dark respiration of the ear was five times greater than net photosynthesis,

Fig. 1

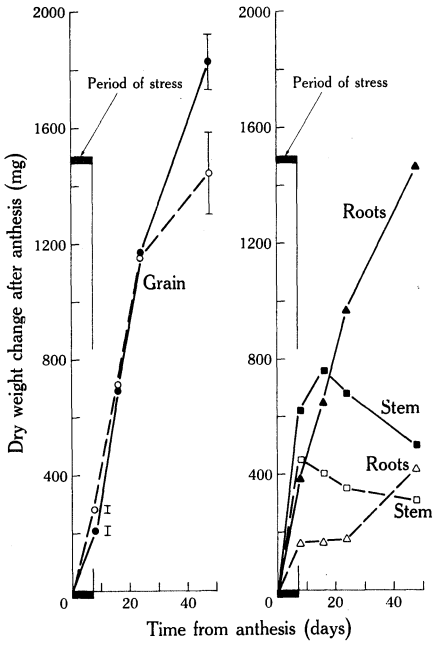


Fig. 2

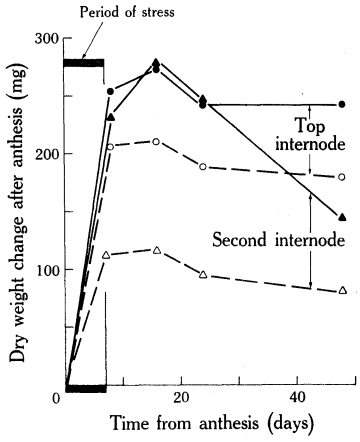
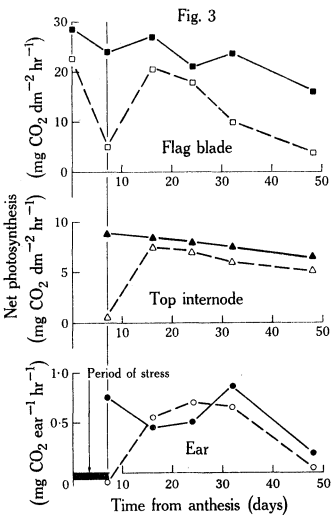


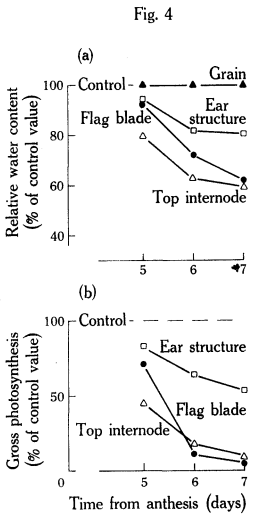
Fig. 1.—Dry weight increase of the roots, stem, and grains per ear of Gabo wheat in relation to water stress after anthesis (broken lines). Controls, solid lines. Each value is the mean of 10 replicates. Vertical lines indicate 2 × S.E.

Fig. 2.—Dry weight change of top internode and second internode from the top in relation to water stress following anthesis (broken lines). Controls, solid lines.

while in the stem dark respiration was one-third of net photosynthesis and in the leaf this value was only one-twelfth of net photosynthesis. The reason for tabulating net photosynthesis in this instance was to provide a basis for assessment of the level of assimilates available for grain growth. In the supplementary experiment the reduction in gross photosynthesis due to stress, estimated as net photosynthesis plus dark respiration, was compared with relative turgidity measurements, established immediately following gas-exchange measurements 5, 6, and 7 days after anthesis (Fig. 4). It is clear that the ear structure was more resistant to desiccation than either the stem or leaf and this was reflected in a greater depression of photosynthesis in the latter two organs.

Following rewatering there was considerable recovery of photosynthesis in all parts (Fig. 3), although the long-term analysis brought out several differences. Firstly, the flag leaf blade showed premature senescence, as did the lower leaves at an earlier stage, as indicated by their rapid rate of yellowing following stress. The top internode was the most resilient of the organs examined, in that on recovery from stress the tissue maintained a high rate of activity until after grain maturation. The ear was intermediate in response, and although the glumes senesced rapidly towards grain maturity, a smaller but similar decline was evident in the ears of non-stressed plants.





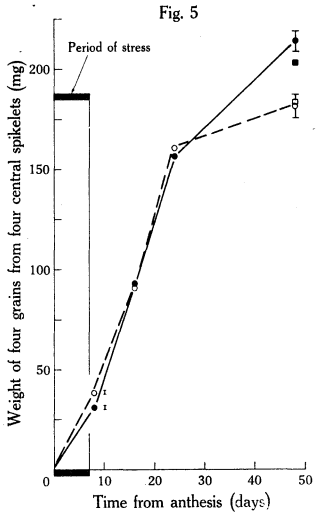


Fig. 3.—Net photosynthesis in the ear, flag leaf blade, and stem of Gabo wheat in control plants (solid lines) and plants subject to water deficiency for the first 7 days after anthesis (broken lines). Each result is the mean of three replicate plants.

Fig. 4.—Relation between relative turgidity (*a*) and gross photosynthesis (*b*) of the ear, top internode, and flag leaf blade of Gabo wheat when watering ceased in stressed plants at anthesis. Each value is the mean of two replicates.

Fig. 5.—Change in individual grain weight in response to water stress. Values are the sum of the weights of the basal grains taken from the four central spikelets in an ear 8 days after anthesis and represent the mean of 10 replicates. ● Controls. ○ Stressed. The mean number of grains set per ear for control and stressed plants was 41 ± 1 and 36 ± 1 respectively and the mean number of cells per endosperm $(125 \pm 7) \times 10^3$ and $(157 \pm 11) \times 10^3$ respectively. The additional values shown on day 48 are for ears in which additional grains were removed at day 10. Mean grain number per ear was 27 for controls (■) and 25 for stressed plants (□) for this treatment. Vertical lines indicate $2 \times$ S.E.

An examination of dry weight increases of the main culm and root system in the first experiment indicated an overall reduction in net assimilation by the stressed plants of 46% for the first 24 days after anthesis, and 75% for the period 24–48 days after anthesis, thus confirming the pattern of accelerating senescence observed in the gas-exchange measurements.

With a small reduction in grain set and greater total grain weight per ear immediately after stress, it was clear that the average weight per grain was initially increased. The response of grains set prior to the initiation of the water deficit is shown in Figure 5. The combined weight of four grains, taken from the basal florets of

the four central spikelets 8 days after anthesis, was significantly increased by stress and these grains showed an enhanced rate of cell division in the endosperm although, as with total grain weight, the final size of individual grains of stressed plants was significantly less than that of controls. The removal of additional grains 10 days after anthesis did not increase the final weight of the remaining grains in stressed ears.

TABLE 1

DRY WEIGHT (MG) OF THE PARTS OF THE WHEAT PLANT IN RELATION TO A PERIOD OF WATER DEFICIT FOR 6 DAYS FOLLOWING ANTHESIS

Each result is the mean of 12 replicates ±S.E.

Plant Part	Anthesis	10 Days after Anthesis		35 Days after Anthesis	
		Control	Stressed	Control	Stressed
Ear structure	522±22	686±25	572±23	630±37	597±27
Total grain	21±2	437±29	392±27	2511±192	1974±120
(No. of grains)	—	(57·5±2·0)	(45·3±1·8)	(53·6±4·0)	(46·4±1·6)
Four central grains	3·4±0·2	42·6±1·1	48·2±1·1	215·1±2·0	190·2±1·9
Top internode	240±15	601±21	400±14	486±27	390±12
Second internode	363±22	757±35	406±15	516±26	401±27
Lower internode	545±64	913±111	622±30	676±36	656±89
Crown	493±35	676±39	556±15	899±69	658±47
Tillers	—	458±72	78±15	7490±768	2025±459
(No. of tillers)	—	(16·5)	(8·8)	(15·7)	(8·3)
Roots	735±43	1021±51	693±30	1130±63	693±28

The results of the second experiment are shown in Table 1, and largely confirm the observations from the first. In this instance grain weight per ear was greater in controls than in stressed plants 10 days after anthesis, but this difference was associated with a much greater reduction in seed set. Examination of individual grains confirmed that these were initially larger following a period of stress, although in the final analysis 35 days after anthesis the position was reversed. The top "growing" internode was less sensitive to stress than the lower "storage" internodes. Tillers showed very much reduced growth and the dry weight of the root system decreased over the stress period and failed to show any recovery 35 days after anthesis.

An analysis of the water status of the plants 6 days after anthesis, that is just before rewatering of the stressed plants, confirmed that the leaf and stem lost water more readily than the ear structure, and the relative turgidity of isolated grains from stressed plants did not differ significantly from the controls, as shown in the following tabulation (each result is the mean of 12 replicates ±S.E.):

	Relative Turgidity (%)	
	Control Plants	Stressed Plants
Flag blade	98±0·1	53±6·4
Top internode	94±1·4	56±1·2
Ear structure	94±0·3	73±2·2
Isolated grains*	78±6·2	74±3·6

* Values not corrected for increases in grain volume due to growth during the water uptake period.

IV. Discussion

The specific object of these experiments was to examine both the short- and long-term effects of a temporary water deficit during the period of rapid cell development in the endosperm of the grain.

Although water stress severely reduced the water content of the leaves, stem, and to a smaller extent that of the ear structure, there was little or no effect on the water content of the grain. This result is similar to that obtained during the period of rapid starch deposition in the grain 15–20 days after anthesis (Wardlaw 1967), and confirms earlier observations by other workers (Konovalov 1959; Aspinall 1965; Kydrev 1969). An explanation for the resistance of the grains to water loss would need further study, but the separation of the endosperm from the vascular tissue, and the observation by Zee and O'Brien (1970) that there is discontinuity of the xylem entering the grain may be relevant.

One feature of stress in these early stages was a significant decrease in grain set, and in confirmation of earlier observations by Konovalov (1959) and Asana and Joseph (1964) a greater initial growth rate of individual grains. This initial increase in grain size under stress conditions was associated with a greater rate of cell division in the endosperm. There is already evidence from the work of Konovalov (1966) and Rawson and Evans (1970) of a correlative inhibition between developing grains in an ear, based on the observation that artificial sterility in a floret at or before anthesis enhances the development of the remaining grains in a spikelet, while a later adjustment of grain number is often without effect (Buttrose and May 1959). Thus the stress effect on grain size could well result indirectly from the effect of stress on grain set.

The increase in weight per grain resulting from stress initially acted as a compensation for reduced seed set, but during the latter stages of development this advantage was lost and grain growth prematurely ceased in stressed plants. Thus at maturity, droughted plants showed a reduction in grain yield (cf. Asana, Saini, and Ray 1958; Aspinall 1965).

Although senescence was accelerated and photosynthesis reduced by stress, the gas-analysis studies indicated that the supply of assimilates from the uppermost parts of the plant were always in excess of grain requirements. Examination of the period from 24 to 40 days after anthesis, when total grain weight per ear in stressed plants increased by about 300 mg, gave the following estimates of dry weight contribution from the various organs. The assumption has been made here that carbon constituted 40% of the plant dry weight. The flag leaf blade, with an area of 25 cm^2, a mean net photosynthesis of 10 mg CO_2 dm^{-2} hr^{-1} for 16 hr at 3500 f.c., and a dark respiration of 0·8 mg CO_2 dm^{-2} hr^{-1} for 8 hr, would yield a net gain of about 418 mg dry weight over the 16-day period. The stem, including the flag sheath, with an area of approximately 35 cm^2, a mean net photosynthesis of 6 mg CO_2 dm^{-2} hr^{-1} for 16 hr light, and a dark respiration of 2 mg CO_2 dm^{-2} hr^{-1} for 8 hr, would yield a net gain of about 76 mg dry weight. Finally, the ear with a mean net photosynthesis of 0·6 mg CO_2 ear^{-1} hr^{-1} for the 16-hr photoperiod and a dark respiration of 1·5 mg CO_2 ear^{-1} hr^{-1} for 8 hr, would yield a net loss of about 26 mg dry weight. The combined total for the 16-day period of 468 mg dry weight was well in excess of the 300 mg actually utilized and this excess was presumably available for root or tiller growth, or respiration in the lower parts of the plant.

The second approach in examining the adequacy of assimilate supply for grain development following water stress was to reduce the total demand for assimilates by removing additional grains from the ear, 10 days after anthesis. Again there was no evidence for a shortage of assimilates, in that the growth of the remaining grains in droughted ears was not enhanced by this treatment. These results also confirm the earlier observations of Buttrose and May (1959) on well-watered plants, that grain removal did not alter the growth of the remaining grains.

The nature of the indirect effect of stress on grain development is unknown. However, enhanced leaf senescence could alter the type and quantity of metabolites, other than sugar, reaching the ear (Tarchevsky 1957; Stutte and Todd 1968). Kesseler (1959) and Kydrev (1966) have evidence for an effect of adenine on the drought response of plants, which could indicate a response mediated through nucleic acid synthesis, and Frazier and Appalanaidu (1965) refer to a paper by Alexandrov and Alexandrova, where it was suggested that disintegration of the endosperm nuclei influences the ripening of the grain.

In many water-stress experiments on cereals the root system has been ignored, but the present analyses indicate the extreme sensitivity of the roots to stress at this stage of development and root function, possibly through reduced cytokinin production (Itai and Vaadia 1965, 1971), may be an important factor in premature senescence of the grains. Some support for the involvement of roots in grain development comes from earlier work on the pattern of seed development in detached culms of the pasture grass *Phalaris tuberosa*, where there was a similar initial rate of seed development to that of intact control plants, but a premature cessation of growth in the later stages (McWilliam and Wardlaw 1965).

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