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Post-Anthesis Sink Size in a High-yielding Dwarf Wheat: Yield Response to Grain Number

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Abstract

Experiments to study the effect of grain number per sq metre on kernel weight and grain yield in a high-yielding dwarf spring wheat (*Triticum aestivum* cv. Yecora 70) were conducted in three seasons (1971–1973) under high-fertility irrigated conditions in north-western Mexico. Crop thinning, shading and carbon dioxide fertilization (reported elsewhere), and crowding treatments, all carried out at or before anthesis, led to a wide range in grain numbers (4000 to 34,000/m^2). Results indicated the response of grain yield to changing sink size (grains per sq metre), with the post-anthesis environment identical for all crops each year, and with all but the thinner crops intercepting most of the post-anthesis solar radiation.

Kernel weight fell linearly with increase in grain number over the whole range of grain numbers studied, but the rate of fall varied with the season. Grain yield, however, increased, reaching a maximum at grain numbers well above those of crops grown with optimal agronomic management but without manipulation. It was concluded that the grain yield in normal crops was limited by both sink and post-anthesis source. There was some doubt, however, as to the interpretation of results from crowded crops, because of likely artificial increases in crop respiration on the one hand, and on the other, in labile carbohydrate reserves in the crops at anthesis. Also deterioration in grain plumpness (hectolitre weight) complicates the simple inference that further gains in yield can come from increased grain numbers alone.

Introduction

In attempts to understand variation in the grain yield of cereals, emphasis in the post-anthesis period of the crop has been placed either on 'source' (the photosynthetic capacity of the crop) or on 'sink' (the capacity of the grains to utilize the products of photosynthesis). A major component of sink is the number of grains (grains per sq metre). More recently the view has arisen that the yield can be limited simultaneously by both source and sink, and that an increase in either one should lead to increased yield (Gifford 1974).

A similar conclusion to the last-mentioned view was reached in field studies with shading, carbon dioxide fertilization, and thinning treatments applied to crops of a high-yielding dwarf wheat (*Triticum aestivum* cv. Yecora 70) grown under irrigation and high fertility in north-western Mexico (Fischer 1975; Fischer and Aguilar 1976; Fischer and Laing 1976; Fischer and Maurer 1976). It was shown that despite the sensitivity of yield to changes in post-anthesis source, control crops appeared to have sufficient unused source capacity to produce a greater grain yield had grain number been greater. This and other considerations led to the suggestion that the most promising avenue for increasing grain yield was via increased sink size or grain number. Although carbon dioxide fertilization and crop cooling before anthesis led to increases in grain number relative to control crops, these increases were relatively small, and a method of achieving greater increases in grain number was sought in order to better test the effect of increased grain number on yield.

Crowding of rice plants in containers has been used to create artificial canopies of differing leaf area indices (Takeda 1961). Crowding may initially produce artificially high crop respiration rates, but this effect is likely to decline rapidly with time after crowding (Ludwig *et al.* 1965). Thus it seemed feasible to use a similar technique with wheat—crowding just before spike emergence—to achieve artificially high grain numbers. Since the major part of grain dry matter comes from photosynthesis after spike emergence (Thorne 1974), grain yield in the crowded crop should receive no *direct* benefit from the conditions experienced by the plants before crowding. Also, since wheat crops here produced very high leaf area indices and achieved almost full light interception (95%) for much of the post-anthesis period (Fischer 1975), crowding is unlikely to further increase the light energy available to the post-anthesis photosynthetic system. Thus the technique of crowding just before the grain-filling period should be a simple way of studying the effects of substantial increases in grain number. Following the report of the results obtained with crowding treatments, this paper combines these data with those of the aforementioned shading and other studies in the same environment, to examine the relationship between grain yield and grain number in the cultivar Yecora 70 over a wide range of grain numbers.

Table 1. Weather for 1970–1973 and long-term means at CIANO, Mexico

Month	Mean temperature (°C)				Solar radiation (Langley/day)			
	1970–71	1971–72	1972–73	Long-term	1970–71	1971–72	1972–73	Long-term
December	16·5	15·5	17·1	16·3	278	284	280	290
January	13·7	15·2	13·9	15·0	331	297	306	312
February	14·6	16·4	16·5	15·8	409	405	359	399
March	18·0	19·9	16·1	17·7	535	523	520	512
April	19·7	21·6	18·7	20·8	602	605	615	594

Materials and Methods

Experiments were conducted at the Centro de Investigaciones Agricolas del Noroeste (CIANO) near Ciudad Obregon, Sonora, Mexico. In this region wheat is grown under irrigation and high fertility, with sowing in November–early December and harvest in April. Weather conditions for the three experimental years (1971–1973) are summarized in Table 1. Crops receiving treatments other than crowding were grown under optimal agronomic management, including 120 kg of seed per hectare, six irrigations, 200–300 kg nitrogen/ha, 60–80 kg phosphorus pentoxide/ha and complete weed and disease control (Fischer 1975).

The crowding technique was similar each year. Yecora 70 was used throughout with the exception of one treatment in 1973 (see Table 2). Seeds were planted in early December in several hundred soil-filled containers partly buried in the soil in the field. In 1971, clay pots of 15 cm diameter were used. A more satisfactory arrangement involving open-ended tubes, 17 cm in diameter by 25 cm tall and made of black Polythene film, was employed in 1972 and 1973. Containers were initially spaced at about two per sq metre in the field. Plants were thinned to six per container in early January. Water and nutrients were applied so as to obtain normal plant growth. However, as a result of inexperience with the technique, lack of water and/or nitrogen caused reduced leaf size, tillering and stature in 1971. Nevertheless, because of the wide spacing of the containers, tillering and spike production was always considerably greater than that of plants in adjacent plots sown at normal densities.

Crowding was carried out when the main shoot spikes were beginning to peep. Immediately before crowding, the clay pots or Polythene tubes were lifted and the respective containers removed. An area of *c.* 2 m^2 of crowded plants was established for each crowding treatment. In 1972 and 1973 the crowded areas were set within

Table 2. Description of crowding treatments (see also text)

Year	Date		Crowding treatment	Container density per m^2	Description
	Sown[A]	Crowded			
1971	9 Dec.	3 Mar.	1	52	High density but smaller plants
1972	4 Dec.	19 Feb.	1	39	High density
			2	25	Low density
			3	39	High density, leaf removal[B]
1973	7 Dec.	23 Feb.	1	29	Moderate density
			2	29	Moderate density, tiller and leaf removal[C]
			3	29	Moderate density, erect genotype[D]

[A] Of previous year.
[B] Removal at crowding of distal half of all leaves of larger tillers so as to create more erectophile canopy.
[C] Removal at crowding of all tillers without flag leaf lamina fully emerged (above ligule of penultimate leaf) and of all leaf lamina except that of flag and penultimate leaf in remaining tillers.
[D] Durum wheat (*Triticum turgidum* L.) selection, known as S-0195, and having short erect leaves.

plots seeded normally; in these cases sufficient plants and soil were removed beforehand from an area within the plot, so that the crowded plants exactly occupied the space evacuated, having the top of their canopy level with that of the surrounding crop. The crowded plants were irrigated frequently because their root systems had been disturbed. Nitrogen (50 kg/ha) was applied to the crowded crops just after crowding in 1971 and 1972.

Various crowding treatments were employed (Table 2). Treatments 1 and 2 in 1972 were intended to see whether there was any response to leaf area index. Treatment 3 in 1972 and 1973 were attempts to favourably modify the canopy of the crowded crop by making it more erectophile. The durum wheat selection (treatment 3, 1973) has very erect leaves, whereas Yecora 70 has rather lax ones. Finally, treatment 2 in 1973 aimed to reduce shoots and leaves which in the crowded situation would have been heavily shaded.

The crowding treatments were not replicated. Sampling in these experiments involved, at the moment of crowding, harvesting all plants from a number of containers selected at random (4, 7 and 12 in 1971, 1972 and 1973 respectively). Total dry weight and photosynthetic area (area of green leaf lamina+half the surface area of green leaf sheath and stems) were determined. At maturity *c.* 1 m^2 was harvested from the centre of the crowded area. This left at least two rows of crowded containers bordering the harvested area on all sides. The area harvested was divided into several portions of equal area, and these were handled separately. Total dry weight, grain dry weight and numerical components of yield were determined on each; means and standard errors of means were calculated. In addition to the above, in 1973 subsamples of dry matter taken, both at crowding and at maturity, were analysed for total soluble sugar content. The subsamples were ground, extracted twice in 80% ethanol at 70° for 1½ hr, and sugars determined by the anthrone method. In all treatments, the dates of 50% anthesis and 50% spike maturity (spikes without green) were determined by counting random samples of shoots.

There was no attempt to maintain uncrowded containers as controls for the crowded ones. Plots seeded at normal densities and grown under optimal management were considered appropriate controls. In all cases these were close to the crowded plants and were seeded at the same date. They are referred to here as control crops.

Descriptions of adjacent experiments involving other treatments and from which some results are drawn can be found in the references already mentioned. However, an experiment in 1972 which used a gametocide (RH531) to vary grain number in Yecora 70 has not been described. Again agronomic management was optimal. The gametocide was applied at around boot stage in concentrations ranging from 100 to 5000 ppm. There were substantial reductions in grain number with the higher concentrations, but no other obvious effects on the crop.

Results

Crowding experiments

Crop Development

In all crowded treatments 5% and 50% anthesis was reached at 6 and 11–12 days respectively after crowding. The date of 50% anthesis corresponded also to the date when 50% spikes had fully emerged above the flag leaf ligule. For Yecora 70, 50% maturity was reached 37, 42 and 47 days later in 1971, 1972 and 1973 respectively, with no effect of treatment. The durum wheat (treatment 3, 1973) was 6 days later in maturity than Yecora 70. Anthesis dates and lengths of the post-anthesis period in control crops were similar to those in the crowded crops.

Photosynthetic Area Index

The photosynthetic area index (PAI) values achieved immediately following crowding were as follows (±SE of mean): 1971, 14·9±1·8; 1972, 30·7±2·6 (1), 19·7±1·6 (2) and 27·5±2·6 (3); and 1973, 18·1±1·1 (1), 7·7±0·9 (2) and 16·6±0·7 (3). Notwithstanding the low precision of these measurements, PAI values were very high, with the exception of treatment 2 in 1973 where trimming had reduced the PAI to a level similar to that of control crops at the same date (10·1, 8·3 and 8·2 in 1971, 1972 and 1973 respectively). Measurement of photosynthetically active radiation at ground level at 10 a.m. on a clear day in 1973 (9 March 1973) showed light transmission to be less than 1% in both control and crowded crops, ranging from 0·1% (crowded, treatment 1) to 0·6% in the control crop of the erect durum wheat.

Grain Yield and Numerical Components

With crowding the number of spikes per sq metre was approximately twice that in control crops (Table 3). The grain number was also considerably greater as a result of crowding but the kernel weight was always lower. The resultant effects of these responses on grain yield were clear yield increases with crowding in 1971 and 1973, but only a small increase in 1972. The yield of the 1971 crowded treatment (1011 g dry grain per m^2) corresponds to a yield of 11·8 t/ha at 14% moisture; the control yield was 8·4 t/ha.

Table 3. Shoot number at crowding and grain yield and yield components at maturity: all crowding treatments plus Yecora 70 control crops

Year and treatment	Shoots[A] per m^2	Spikes per m^2	Grains per spike	Grain no. ($1000/m^2$)	Kernel wt. (mg)	Grain dry wt. (g/m^2)
1971						
Control	810	489	39	19·1	38·2	727
Crowded 1	2500	1250	27	33·6	30·1	1011
SE mean[B]	115	NA	NA	NA	0·2	NA
1972						
Control	960	462	38	17·7	35·4	650
Crowded 1	2475	1029	25	26·0	28·2	732
2	1585	777	33	25·7	27·2	699
3	2475	1191	24	29·0	22·8	662
SE mean[B]	195	46	1	1·0	0·7	25
1973						
Control	738	487	31	15·0	45·4	681
Crowded 1	2220	1020	29	29·1	32·9	956
2	1210	822	35	28·5	29·5	839
3	2070	1016	25	25·2	38·6	973
SE mean[B]	67	31	1	0·6	1·0	53

[A] Immediately after crowding, or at that date for control crop of Yecora 70.
[B] Refers to crowded treatment means; NA, not possible to analyse.

In 1972 there was little response to density of crowding (treatment 2 *v.* 1), the greater density (1) leading to more spikes but no more grains per sq metre, because the number of grains per spike fell. Leaf removal with crowding (treatment 3) somewhat lowered the yield, owing to a significant reduction in kernel weight. In 1973 tiller and leaf trimming (2) also caused lower yields associated with significantly lighter kernels. The crowded durum wheat (3) attained the same yield as the crowded bread wheat (1) through having fewer, but heavier, kernels.

Dry Matter Production and Distribution

Control crops showed a net accumulation of from 700 to 900 g dry matter (above ground) per sq metre from the date of crowding until maturity (Table 4); the grain yield was 5–27% less than this figure. The crowded crops accumulated somewhat less dry matter than the control crops in 1971 and 1973; in 1972 the net accumulation in the crowded crops was very small, and this was associated with a higher apparent weight loss from the leaf plus stem fraction. Grain yields in crowded crops always exceeded the net dry matter accumulation after crowding, the difference arising from substantial reductions in the weight of leaf plus stem over the period crowding to maturity.

Immediately after crowding in 1973, measurements showed the following quantities of total soluble sugars: treatment 1, 220 g/m^2; treatment 2, 147 g/m^2; treatment 3, 188 g/m^2. At maturity the quantity was less than 25 g/m^2 (2–3 % of stem weight) for all three crowded treatments, whereas control crops contained 60–80 g/m^2 (14–18 % of stem weight).

Table 4. Above-ground dry weight and its components at crowding and at maturity; all crowding treatments plus Yecora 70 control crops

Year and treatment	Dry weight (g/m^2): Immediately after crowding: Total	Leaf + stem	Spike	At maturity: Total	Leaf + stem	Spike[A]	Grain	Change in total
1971								
Control	950	950		1712	691	294	727	762
Crowded 1	2167	2167		2907	1267	629	1011	740
SE mean[B]	153	NA		NA	NA	NA	NA	
1972								
Control	600	600		1475	587	238	650	875
Crowded 1	2950	2340	610	3000	1758	510	732	30
2	1890	1498	362	2215	1117	399	699	325
3	2760	2150	610	2857	1615	580	662	97
SE mean[B]	277	218	82	96	46	23	25	
1973								
Control	738	616	122	1670	729	260	681	932
Crowded 1	2183	1810	373	3001	1495	549	956	818
2	1475	1102	373	2234	935	460	839	759
3	2170	1701	469	2993	1331	690	973	823
SE mean[B]	100	81	38	131	56	51	53	

[A] Grain excluded.
[B] Refers to crowded treatment means; NA, not possible to analyse.

Root weights were measured in 1973 only. Averaged over the three crowding treatments, the dry weight of plant crowns plus roots, recoverable from the soil of the container in which the plants were grown, decreased in the crowded crops from 395$\pm$20 g/m^2 immediately after crowding to 347$\pm$15 g/m^2 at maturity. Over a similar period crop crown and root weights in the controls would probably have risen slightly (R. A. Fischer, unpublished data from control crops in 1971, 1972 and 1974).

Relationship of grain yield and kernel weight to grain number

Other experiments in which the grain number of Yecora 70 varied were conducted each year. Early shading or heating of the crop reduced the grain number (Fischer 1975; Fischer and Maurer 1976); early carbon dioxide fertilization or cooling of the crop increased the grain number (Fischer and Aguilar 1976). Crop thinning treatments also reduced the grain number (Fischer and Laing 1976). These results, along with those from the crowding experiment, permit an examination of the effect of wide variation in grain number on grain yield and kernel weight (Fig. 1). Only data from shading, carbon dioxide fertilization and temperature treatments which had terminated at least 2 weeks before anthesis, and from thinning treatments which were carried out at or before anthesis, were used. Also crowded crops which had leaves or tillers removed were excluded. All crops reached anthesis within a few days of each other in any year, so that grain filling took place under identical weather conditions.

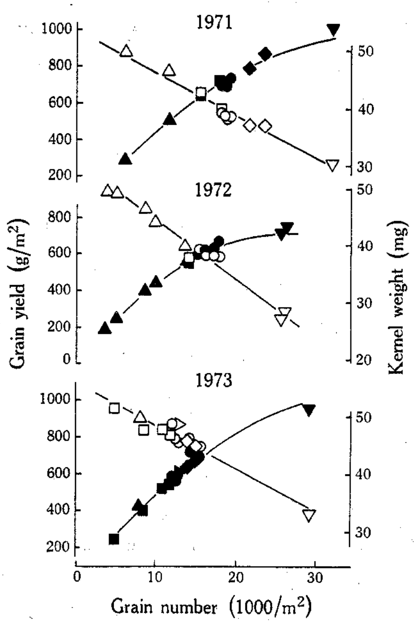

Fig. 1. Relationship of kernel weight (open symbols) and grain yield (solid symbols) to grain number for Yecora 70 in 1971, 1972 and 1973. Treatments shown thus: control (○); shading (□); thinning(△); crowding (▽); CO_2 fertilization (◇); cooling (▷).

General relationships are evident each year, with a considerable degree of similarity between those of 1971 and 1973 (Fig. 1). Linear regressions fitted to the values of kernel weight (Y, mg) and grain number (X, $1000/m^2$) were as follows:

1971 $Y = 53{\cdot}1 - 0{\cdot}73X$ $(r^2 = 0{\cdot}94)$

1972 $Y = 54{\cdot}5 - 1{\cdot}04X$ $(r^2 = 0{\cdot}98)$

1973 $Y = 55{\cdot}9 - 0{\cdot}76X$ $(r^2 = 0{\cdot}95)$.

Thus the reduction in kernel weight with increase in grain number was clearly greater in 1972. The relationship for 1972 is confirmed by the gametocide experiment, when the corresponding regression was

$$Y = 52{\cdot}7 - 0{\cdot}92X \qquad (r^2 = 0{\cdot}92).$$

Despite reductions in kernel weight, yield increased with increase in grain number to above control crop values in all years. The grain number giving maximum grain yield is estimated by these linear regressions to have been near $36{,}000/m^2$ in 1971 and 1973, but only 26,000 in 1972.

Discussion

Crowding

Results suggest that, as assumed initially, crowded crops would not have intercepted any more solar radiation during grain filling than control crops. However, contrary to expectations, crop respiration may have been considerably higher in crowded crops than in control ones. The net total dry weight gain was greater in control crops each year and was significantly greater at the lower pot density (2) than at the higher one (1) in 1972 (Table 4).

Such results can be explained if there is a substantial amount of crop respiration which is proportional to crop dry weight. This component of respiration is usually defined as maintenance respiration (McCree 1974); his data suggest a maintenance coefficient (grams dry matter respired/gram total dry weight/24 hr) of around 0·01 as appropriate for wheat at the mean temperatures obtaining here (17–20°C). Consideration of the differences in total dry weight between crowded (treatment 1) and control crops in Table 4 points to 600–1000 g/m^2 more maintenance respiration from crowding to maturity (calculated at 0·01/day) in the former case. A second component of respiration is growth respiration (McCree 1974). Since this is a fixed and substantial proportion of the amount of growth, in this case largely grain growth, growth respiration would also have been greater with crowding.

Overall then, it seems that crop respiration (growth plus maintenance) would have been considerably higher in the crowded crops, such that gross photosynthesis in these crops (net dry weight gain plus respiration) would undoubtedly have surpassed gross photosynthesis in the control crops in 1971 and 1973, and probably also in 1972. The different result in 1972 may reflect the higher mean temperature after crowding in that year (18·5, 19·9 and 16·9°C for 1971, 1972 and 1973 respectively), since maintenance respiration is strongly dependent on temperature (McCree 1974). Greater gross photosynthesis with crowding could result from the greater number of grains and hence greater demand or sink for photosynthate (Rawson *et al.* 1976).

Greater maintenance respiration losses would have disadvantaged the crowded crops relative to control crops in terms of the original hypothesis. On the other hand, greater amounts of sugar reserves present in the plants at crowding would have given crowded crops an artificial advantage. Reserves of 200 g/m^2 in 1973 immediately after crowding, compare with estimated reserves of about 40 g/m^2 in control crops at 10 days before ear emergence (estimates based on serial sampling of control crops in 1974 and 1975, R. A. Fischer, unpublished data). Thus the advantage for the crowded crops was probably small (about 160 g/m^2) relative to their disadvantage in terms of subsequent respiratory losses. Nevertheless in treatment 2 in 1973 the removal of a large quantity of tissue (700 g/m^2, including 73 g/m^2 of sugar reserves) actually tended to lower the yield. The material removed would have contributed mobile reserves on the one hand, and respiratory losses probably well in excess of its gross photosynthesis on the other. Apparently the former effect was greater than the latter, perhaps because other compounds, in addition to sugars soluble in 80% ethanol, can contribute to grain filling when the demand is great. Also sugar reserves, regardless of when they were formed, were utilized more fully by the crowded crops as indicated by their lower stem sugar levels at maturity. Such an effect would seem a valid although unanticipated response to increased sink size. All these effects complicate the simple assumption that crowding measures the effect of increased grains per sq metre on the utilization of a given quantity of radiation intercepted by the crop, through sink size effects on gross photosynthesis.

Relationship to Grain Number

Notwithstanding the aforementioned complications, Fig. 1 shows a surprising degree of continuity between the data from crowding treatments and that of other treatments. Kernel weight fell continuously as grain number increased from very low values. Similar treatments (but not crowding) were carried out in 1973–74 and 1974–75. The corresponding regressions of kernel weight (Y, mg) on grain number (X, $1000/m^2$) were:

1974 $Y = 57\cdot8 - 0\cdot90X$ ($r^2 = 0\cdot76$; X range 6·8–17·6; number of crops, 23);

1975 $Y = 56\cdot8 - 0\cdot62X$ ($r^2 = 0\cdot56$; X range 4·0–19·2; number of crops, 20).

The decline in kernel weight with increasing grain number each year no doubt reflects increasing post-anthesis intergrain competition. There exists the possibility that the pre-anthesis treatments used here also modified the potential of the grains to grow, for example by effects on the size of the floret parts. The continuity of points in Fig. 1, and the indication from extrapolation to zero grain number (zero intergrain competition) of similar potential kernel weights (53–57 mg) in each season, are taken to suggest that such pre-anthesis effects were minor.

Given that all crops were well fertilized and irrigated, it is reasonable to assume that the intergrain competition referred to above is dominated by competition for carbohydrate, supplied largely but not entirely by post-anthesis photosynthesis. Light intercepted by the crop per grain during the post-anthesis period would have declined monotonically with increased grain number in each season (measurements suggested that 95% light interception at anthesis was associated with crops having grain numbers of about $12{,}000/m^2$). The fact that the kernel weight *v.* grain number relationships of Fig. 1 were always close to linear is probably the consequence of a fortuitous combination of these changes in light interception per grain and the response of photosynthesis and mobilization to increased sink size.

The seasonal variation in slope of the kernel weight *v.* grain number relationship appears, with the exception of 1971, to show a good inverse relationship with mean grain-filling temperature. The respective values of slope and temperature were: 1972 (1·04, 20·6°C), 1973 (0·76, 16·7°C), 1974 (0·90, 18·0°C) and 1975 (0·62, 16·8°C). This is consistent with the hypothesis that increased grain-filling temperature increases the degree of source limitation (Sofield *et al.* 1974; Fischer and Laing 1976), and hence increases the intensity of intergrain competition at any given grain number. However, the slope value for 1971 (0·73, 19·7°C) cannot be explained. Results from shading and thinning experiments, the extrapolated value of kernel weight at zero grain number, and the temperature, all suggest that 1971 should have been fairly similar to 1972.

The most significant result in Fig. 1 is that, although kernel weight fell, the grain yield increased with increases in the grain number above the levels of control crops ($14{,}000$–$19{,}000/m^2$). This was especially so in 1971 and 1973 (and by extrapolation 1974 and 1975), when the maximum grain yield would have been reached at grain numbers well above $30{,}000/m^2$. Greater grain yield resulted therefore from increased sink size (grain number), with source, at least in terms of radiation intercepted, held constant. As discussed earlier, the extra dry matter probably came largely from increased concurrent photosynthesis in response to the greater sink, but greater mobilization of soluble sugar reserves would also have contributed.

Consideration of Fig. 1 shows that for a crop completely limited by sink size the yield relationship must be a straight line through the origin (constant kernel weight); conversely, a horizontal yield *v.* grain number relationship indicates complete source limitation. The control crops here were intermediate, being limited by both sink and source. Simultaneous sink and source limitation appears to be a common situation in wheat crops (Gifford 1974; Fischer 1975), and does not permit an easy conclusion as the best path for further yield improvement.

The fact that control crops produce less grains than necessary to maximize their grain yield points to increased grain number as an avenue for yield increase. However, this apparently wasteful situation is the likely consequence of natural and artificial selection which has favoured plump, well-filled kernels, and presumably a high hectolitre weight which is deemed a desirable aspect of industrial quality. The mechanism appears to be a great sensitivity of grain number to pre-anthesis competitive stresses, whether light, nutrients or water stresses. Grain numbers are reduced so that grain filling is assured.

Hectolitre weight and kernel weight appear to be closely associated within any cultivar (Ghaderi and Everson 1971). For all crops in 1971 the relationship between hectolitre weight (Y, kg/hl) and kernel weight (X, mg) was

$$Y = 36 + 1\cdot 8X - 0\cdot 0018X^2 \ (R^2 = 0\cdot 98,\ n = 14).$$

For example the very high-yielding crowded crop in 1971 had a poor hectolitre weight (74 kg/hl) compared with control crops (80 kg/hl). The desirability of maintaining hectolitre weight creates a dilemma, for it seems that plump grains only arise when the source/sink ratio during grain filling is considerably higher than that giving maximum grain yield. In the past, yield improvement through breeding has resulted from increased grain numbers, but kernel weight, grain plumpness and hectolitre weight have been maintained (Aguilar and Fischer 1975). It would appear therefore that as grain number was increased, post-anthesis photosynthetic capacity also increased, displacing the curves of Fig. 1 upwards. As long as grain plumpness remains an important aspect of quality, further improvements in yield cannot involve large increases in grain number without associated increases in photosynthetic capacity.

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