

# Shading effects on the yield of an Argentinian wheat cultivar

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## SUMMARY

Shading treatments of 50% of the incident radiation were applied to the semidwarf wheat cultivar Leones INTA before and after anthesis in two field experiments in Argentina in 1987 and 1988. The treatments reduced biological (above-ground dry matter) yield, grain yield and number of grains/m<sup>2</sup>. Number of grains/m<sup>2</sup> was closely and linearly correlated with ear dry weight at anthesis and with the photothermal quotient, calculated from 20 days before to 10 days after anthesis. Grain yield was sink limited, and the shading treatments reduced sink strength. The contribution of preanthesis assimilates to grain yield was smaller in the shaded crops than in the unshaded controls; in unshaded crops, almost 40% of grain yield was contributed by preanthesis assimilates whilst in preanthesis shaded crops this contribution was negligible. The proportion of preanthesis assimilates contributed to the grain was closely related to the decrease in stem dry weight during grain filling. The effects of shading on main stems and tillers were the same.

## INTRODUCTION

Grain yields of wheat (*Triticum aestivum* L.) crops under otherwise optimum conditions are sensitive to fluctuations in solar radiation (Fischer 1975; Fischer & Stockman 1980), and variations in grain yield between different environments can often be related to differences in the number of grains/m<sup>2</sup> (Fischer 1975; Thorne & Wood 1987). Fischer (1985) observed that number of grains per unit area was linearly related to the amount of solar radiation received by the crop before anthesis. The effects of shading on number of grains/m<sup>2</sup> could be traced back to reductions in both ear dry weight and number of fertile flowers at anthesis (Stockman *et al.* 1983).

The most sensitive period for the effect was the 20 days before anthesis (Fischer & Stockman 1980), when the stem and ear were elongating rapidly and the florets were being differentiated and maturing. During this phase, a proportion of florets and tillers dies. The period is therefore important in establishing number of grains and hence grain yield (Kirby 1988). However, the grain-setting period should not be ignored: several authors have shown that postanthesis stress also affects number of grains/m<sup>2</sup> (Wardlaw 1970; Jenner 1979).

The effects of other environmental factors on the production and survival of tillers have been reported,

e.g. nutrient concentration (Coaldrake & Pearson 1985), carbon dioxide (Fischer & Aguilar 1976), radiation intensity (Fischer 1975; Thorne & Wood 1987), temperature (Thorne & Wood 1987) and light quality (Casal 1988). The contributions of each shoot category to grain yield have been measured by Thorne & Wood (1988), but changes in growth and yield of different shoot categories under stress do not seem to have been reported. This paper reports the effects of shading at different stages of growth on (i) biological (above-ground dry matter) yield, and grain yield and its components, (ii) the proportion of grain dry matter supplied by preanthesis assimilation and (iii) on the growth of different shoot categories.

## MATERIALS AND METHODS

Experiments were conducted in 1987 and 1988 at the experimental field of the University of Buenos Aires (34° 35' S, 58° 29' W; 25 m above sea level). Total incident short-wave radiation was measured with a piranometer (Kipp & Zonen XR4, Delft, Netherlands) at a meteorological station c. 200 m from the experimental site and converted to incident photosynthetically active radiation (PAR) using a factor of 0.4475, as suggested by Howell *et al.* (1983). The study involved the semidwarf cultivar Leones INTA. The soil was a silty clay loam (Aeric Argiudoll).

### Experiment 1

This experiment was sown by hand on 20 July 1987 at 420 seeds/m<sup>2</sup> in plots of 11 rows, 0.20 m apart and 2.20 m long, distributed in a randomized complete block design with three replicates. After emergence, Zadoks growth stage (GS) 11 (Tottman 1987), plots were thinned to 300 plants/m<sup>2</sup>. Urea (48% N) was applied to all plots at 50 kg/ha at sowing and at 260 kg/ha at the end of tillering (GS 26).

The following treatments were applied: S<sub>0</sub>, unshaded control; S<sub>1</sub>, shaded from beginning of stem elongation (GS 26) to anthesis (GS 64); S<sub>2</sub>, shaded from anthesis to maturity (GS 94); and S<sub>3</sub>, shaded from beginning of stem elongation to maturity. Shading was by means of a black Sarlan shade cloth that decreased light intensity by 50 ± 3%. Shades were suspended 20 cm above the top of the canopy. Temperature measurements indicated that air temperatures in unshaded plots were only c. 1 °C greater than in shaded plots.

### Experiment 2

This experiment was sown by hand on 2 August 1988 at 450 seeds/m<sup>2</sup> in plots of five rows, 0.15 m apart and 2.00 m long, distributed in a randomized complete block design with three replicates. After emergence (GS 11), plots were thinned to 380 plants/m<sup>2</sup>. Diammonium phosphate (46% P, 18% N) was applied before sowing at 50 kg/ha, and urea (48% N) at the end of tillering (GS 26) at 200 kg/ha. The S<sub>0</sub> and S<sub>1</sub> treatments were applied.

Both experiments were treated with fungicides to control diseases, and weeds were removed by hand. At anthesis and physiological maturity, all above-ground biomass was harvested on one central row from a 0.5 × 0.2 m quadrat in 1987, and a 0.5 × 0.15 m quadrat

in 1988. Plant material was divided into laminae, stems (including leaf sheaths) and ears, and was oven dried (70 °C for 4 days) and weighed. Grain yield and its components were also determined at maturity. In Expt 2, plant material was also separated into main shoots and tillers.

The photothermal quotient, the ratio of mean daily radiation: mean daily temperature > 4.5 °C, was calculated as described by Fischer (1985), from 20 days before anthesis (GS 33) to 10 days after anthesis (GS 72). The contribution of preanthesis assimilates to grain yield was calculated as described by Gallagher *et al.* (1975), i.e. the difference between grain yield and total shoot dry matter accumulation from anthesis to maturity.

The ratio of number of grains/m<sup>2</sup>: biomass accumulation during grain filling was used as an estimate of the sink-source relationship throughout the treatments. The data from the two field experiments were subjected to analysis of variance. The degree of association between different traits was estimated by linear regression models.

## RESULTS

Although the 1988 crop was sown 13 days later than in 1987, its date of anthesis was only 2 days later (22 October in 1987 compared with 24 October for 1988). The biological yield and the grain yield of the unshaded control treatments were 35% greater in 1988 than in 1987 (Table 1). The total amount of incident PAR was 10% greater (926 MJ/m<sup>2</sup> in 1987 and 1017 MJ/m<sup>2</sup> in 1988) and the amount of water available during the growing season was 20% greater in 1988 than in 1987. There were no differences between years in harvest index and individual grain weight (Table 1) in the unshaded controls. The differences in grain yield between the 2 years were,

Table 1. Effect of shading on yield and harvest index in the wheat cultivar *Leones INTA* grown in Argentina

Treatment*	Dry matter (g/m <sup>2</sup> )		Harvest index (%)	Number of ears/m <sup>2</sup>	Number of grains/ear	Mean single-grain mass (mg)
	Shoot total	Grains				
1987						
S <sub>0</sub>	943	415	43.7	375	38.9	28.8
S <sub>1</sub>	756	304	40.0	438	26.1	27.5
S <sub>2</sub>	738	289	39.0	370	32.5	24.3
S <sub>3</sub>	620	255	41.3	372	28.0	24.7
s.e.	16	5	0.4	31	2.2	0.3
1988						
S <sub>0</sub>	1503	619	41.2	658	33.4	28.3
S <sub>1</sub>	1360	491	36.1	649	27.0	28.1
s.e.	114	53	0.7	68	1.6	1.0

\* (S<sub>0</sub>) no shading; shading from beginning of stem elongation to anthesis (S<sub>1</sub>), from anthesis to maturity (S<sub>2</sub>) and from beginning of stem elongation to maturity (S<sub>3</sub>).

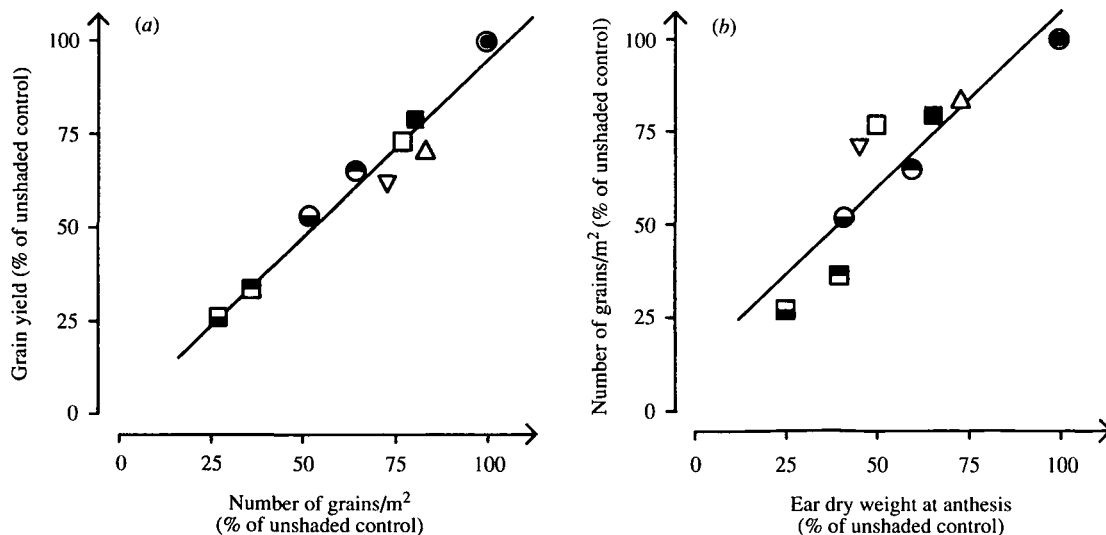


Fig. 1. Relationship between number of grains/m<sup>2</sup> and (a) grain yield/m<sup>2</sup> ( $r^2 = 0.88$ , 8 D.F.) and (b) ear dry weight/m<sup>2</sup> at anthesis ( $r^2 = 0.81$ , 8 D.F.) in the wheat cultivar Leones INTA grown in Argentina in 1987 (open symbols) and 1988 (solid symbols), unshaded (○, ●), or shaded from the beginning of stem elongation to anthesis (□, ■), from anthesis to maturity (△) and from the beginning of stem elongation to maturity (▽). In 1988, main shoot (●, ■) and tiller (○, □) values were identified for the plants unshaded (circles) and shaded from the beginning of stem elongation to anthesis (squares) treatments.

therefore, due to differences in the number of grains/m<sup>2</sup>.

#### Shading before and after anthesis

Shading prior to anthesis only slightly delayed the date of anthesis, by one day in 1987 and 3 days in 1988. Biological yield and grain yield were reduced by shading. Both were significantly and positively correlated with total incident PAR during the growing season ( $r^2 = 0.88$ , 4 D.F.;  $r^2 = 0.93$ , 4 D.F., respectively). Averaged over 2 years, preanthesis shading reduced the incident PAR by 11%, and biological yield was reduced by 15% and grain yield by 24%. Harvest index was also reduced, by 9%, by preanthesis shading (Table 1).

Changes in grain yield produced by shading treatments closely paralleled the changes in the number of grains/m<sup>2</sup> (Fig. 1a). The differences in the number of grains/m<sup>2</sup> were associated with differences in ear dry weight at anthesis (Fig. 1b) and were positively correlated with the photothermal quotient calculated for the period from the beginning of rapid ear growth to the beginning of grain filling (Fig. 2). This interval for the quotient was chosen to include the important phase of grain set.

The S<sub>2</sub> treatment, which was imposed at anthesis, also reduced ear dry weight at anthesis. No explanation can be offered for this and so discussion is concentrated on the effect of photothermal quotient on the number of grains/m<sup>2</sup>.

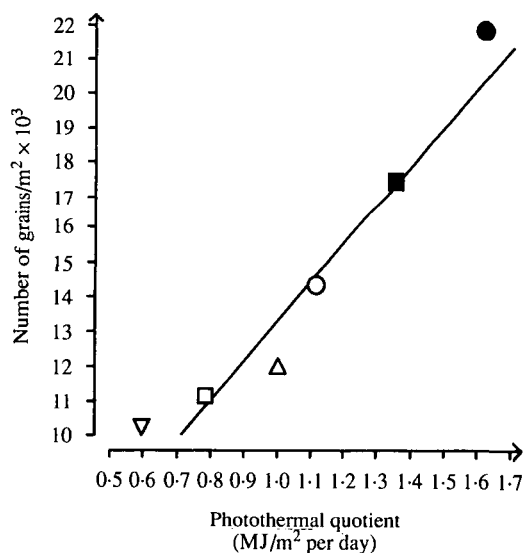


Fig. 2. Relationship between the number of grains/m<sup>2</sup> and the photothermal quotient calculated between 20 days before to 10 days after anthesis ( $r^2 = 0.90$ , 4 D.F.) in the wheat cultivar Leones INTA grown in Argentina in 1987 (open symbols) and 1988 (solid symbols), unshaded (○, ●), and shaded from the beginning of stem elongation to anthesis (□, ■), from anthesis to maturity (△) and from the beginning of stem elongation to maturity (▽).

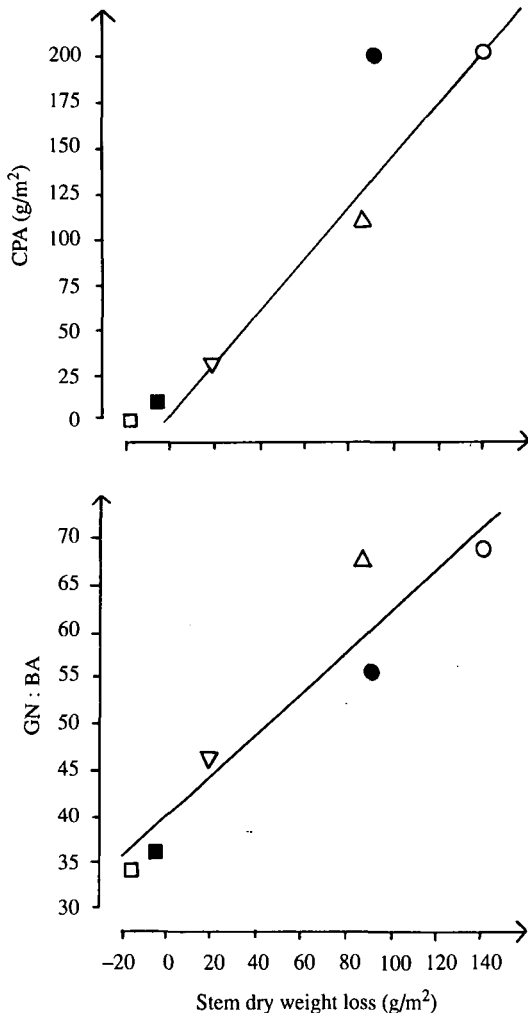


Fig. 3. Relationship between (a) the contribution of preanthesis assimilates to grain yield (CPA) and stem dry weight loss during grain filling ( $r^2 = 0.90$ , 4 D.F.), and (b) between the ratio of number of grains/m<sup>2</sup>:biomass accumulation (g) after anthesis (GN:BA) and stem dry weight loss ( $r^2 = 0.90$ , 4 D.F.) in the wheat cultivar Leones INTA grown in Argentina in 1987 (open symbols) and 1988 (solid symbols), unshaded (○, ●), or shaded from the beginning of stem elongation to anthesis (□, ■), from anthesis to maturity (△) and from the beginning of stem elongation to maturity (▽).

Differences in the number of grains/m<sup>2</sup> within each year were related more to differences in the number of grains/ear than to differences in the number of ears/m<sup>2</sup>. When each value was expressed as a percentage of its respective control value for each year, there was a significant, positive correlation between number of grains/m<sup>2</sup> and number of grains/ear ( $r^2 = 0.90$ , 4 D.F.) but no correlation was found between the number of grains/m<sup>2</sup> and the number of

ears/m<sup>2</sup> ( $r^2 = 0.06$ , 4 D.F.). Postanthesis shading slightly reduced individual grain weight, but pre-anthesis shading had no effect (Table 1).

#### Dry matter growth and grain yield

Grain yields for the S<sub>1</sub> and S<sub>3</sub> treatments were almost equal to net increases in amounts of shoot biomass between anthesis and maturity, indicating little or no contribution of preanthesis assimilates to grain yield (Fig. 3a). Grain yields of the S<sub>0</sub> and S<sub>2</sub> treatments were greater than net increments in biomass between anthesis and maturity, the difference being greatest in the control crops. Thus, the contribution of pre-anthesis assimilates to grain growth and grain yield increased in the following order: S<sub>0</sub> > S<sub>2</sub> > S<sub>3</sub> > S<sub>1</sub> (Fig. 3a). There was a net loss in stem dry weight between anthesis and maturity in all treatments except S<sub>1</sub>, in which it increased. Stem losses were greater in the S<sub>0</sub> treatment than in S<sub>2</sub>, and greater in S<sub>2</sub> than in S<sub>3</sub> (Fig. 3). Therefore, the contribution of preanthesis assimilates to grain growth was positively correlated with the losses in stem dry weight between anthesis and maturity (Fig. 3a). The ratio of number of grains:biomass accumulated during grain filling was positively correlated with the loss in stem dry weight after anthesis (Fig. 3b). Thus, unshaded crops showed the greatest imbalance between sources and sinks for assimilate within the crop (Fig. 3b).

#### Shading within different shoot categories

Preanthesis shading had similar effects on main shoots and tillers and did not alter the relative contribution of each shoot category to the total biological yield, grain yield and number of grains/m<sup>2</sup> of the crop (Table 2). There were no shoot category × shading interactions in the analyses of variance for total shoot dry weight, grain yield, and number of grains/m<sup>2</sup> at physiological maturity.

The relationships between grain yield and number of grains/m<sup>2</sup> and ear dry weight at anthesis for each shoot category were similar to those observed for all categories combined (Fig. 1).

## DISCUSSION

Biological yields decreased in direct proportion to the decrease in incident PAR. It has been suggested by Gallagher & Biscoe (1978) that biological yields are strongly correlated with the total amount of intercepted PAR from emergence to maturity.

Grain yields also decreased in direct proportion to the decrease in incident PAR. Preanthesis shading reduced grain yield by decreasing the number of grains/m<sup>2</sup> and postanthesis shading reduced grain yield by decreasing both grain weight and number of grains/m<sup>2</sup> (Fig. 1a). The shading treatments reduced

Table 2. Contributions to total crop yield of main shoots and tillers of the wheat cultivar Leones INTA grown in Argentina in 1988

Treatment	Total shoot dry matter		Grain yield		Number of grains	
	g/m <sup>2</sup>	%	g/m <sup>2</sup>	%	m <sup>2</sup>	%
Unshaded						
Main shoots	926	61.6	406	65.5	13938	63.6
Tillers	577	38.4	214	34.5	7973	36.4
Shaded before anthesis						
Main shoots	856	62.9	332	67.6	11471	65.7
Tillers	504	37.1	159	32.3	5986	34.3

harvest index because they were applied close to the stage of maximum crop weight and, therefore, affected grain yield more than biological yield. The results were similar to those of Fischer (1975) and Stockman *et al.* (1983).

Number of grains/m<sup>2</sup> has been shown to be reduced by shading during ear growth (Fischer 1975; Fischer & Stockman 1980; Stockman *et al.* 1983; Fischer 1985). In our experiments, the reductions in the number of grains/m<sup>2</sup> due to shading were associated more with reductions in the number of grains/ear than with changes in the number of ears/m<sup>2</sup>. Shading, therefore, predominantly affected ear growth rather than ear survival (Table 1).

Number of grains/m<sup>2</sup> appeared to depend strongly on the photothermal quotient during ear growth and grain set (Fig. 2), calculated here from 20 days before to 10 days after anthesis. Radiation seems to affect number of grains/m<sup>2</sup> through its effect on crop growth rate, and temperature positively affects the rate of crop development (Fischer 1985). Fischer (1985) and Thorne & Wood (1987) in their calculations considered only the period before anthesis. We have included the early phase of grain set because stresses during this period could also affect the number of grains/m<sup>2</sup>. Wardlaw (1970) showed that high incident radiation and low temperatures during the 10 days after anthesis increase grain set and number of grains. The grain-setting period for Leones INTA (the cultivar used in this study) was also 10 days (M. MacManey, unpublished).

The gradient of the linear regression relating number of grains/m<sup>2</sup> to the photothermal quotient was  $11360 \pm 1642$  (Fig. 2), similar to that of 13564 quoted by Fischer (1985), when corrected to consider PAR instead of solar radiation as in Howell *et al.* (1983). However, both values are smaller than the 20700 quoted by Thorne & Wood (1987) from a glasshouse experiment. The lower gradient under field conditions could be expected where many factors, except for incoming radiation, remained uncontrolled. Number of grains produced per unit of photothermal

quotient under field conditions therefore seems to be a conservative quantity, with a possible slight influence of genotype. Assuming that well-managed wheat crops intercept incoming radiation fully during stem elongation, there might be a chance to increase grain yield by inducing anthesis earlier in the season, wherever harmful effects could be avoided (e.g. frost damage), as the photothermal quotient is greater in cold than in warm seasons. A similar conclusion was reached by Fischer (1985) in predicting the date of anthesis for maximum number of grains/m<sup>2</sup> in north-west Mexico. Thus, it is suggested that future breeding programmes aimed at increasing the number of grains/m<sup>2</sup> could introduce cold resistance during stem elongation and anthesis as a possible selection criterion, so that this critical period was in late winter or early spring. This would also result in the grain-filling period occurring under low-temperature conditions, and higher individual grain weight would be expected.

Number of grains/m<sup>2</sup> was reduced when the crop was shaded from anthesis to maturity (Table 1). Jenner (1979) has shown that reductions in irradiance at, or soon after, anthesis reduce the number of developing grains and grain weight. In 1987, there were 3 days of extremely low radiation immediately after anthesis (7.29, 4.15 and 2.34 MJ/m<sup>2</sup> per day). Fischer (1975) and Wall (1979) suggested that low radiation affects the number of grains by decreasing sugar reserves. As has been shown in other studies (Fischer 1985; Thorne & Wood 1987; Slafer & Andrade 1989), grain yield in our study was strongly correlated with number of grains per unit area (Fig. 1a). This suggests that in our study the capacity of the grains to accept assimilate (i.e. sink strength) was more important in determining yield than the supply of assimilates to growing grains (i.e. source strength), as found by Wall (1979) and Thorne & Wood (1987). Slafer & Andrade (1989) concluded that Argentinian wheat-breeding programmes have tended to increase grain yield largely through increases in the number of grains/m<sup>2</sup>. In our experiments, the

reductions in the number of grains per unit area, induced by shading, were not accompanied by increases in grain weight (Table 1).

There are two potential sources of assimilates to supply the grain: that produced by current photosynthesis during grain filling, and remobilization from vegetative tissues to the grain of assimilates produced prior to anthesis. Preanthesis assimilation could provide a buffer of assimilate to sustain grain growth when the demand exceeds postanthesis assimilation (Gallagher *et al.* 1975; Austin *et al.* 1977; Austin *et al.* 1980; Hall *et al.* 1989). The contribution of preanthesis assimilates to grain yield can be estimated from changes in biomass yield between anthesis and maturity (Gallagher *et al.* 1975). Estimates indicate that the contribution of preanthesis assimilates to grain growth were *c.* 49, 38 and 36%, in the S<sub>0</sub> treatment in 1987, in the S<sub>2</sub> treatment in 1987 and in the S<sub>0</sub> treatment in 1988, respectively. Although postanthesis shading (S<sub>2</sub>) reduced total biomass production during grain filling by 16%, the decrease in the number of grains/m<sup>2</sup> was even greater (31%) and, thus, the contribution of preanthesis assimilates to grain growth of the crop shaded after anthesis was smaller (22%) than that of the unshaded control. There was little contribution of preanthesis assimilates to grain growth in the S<sub>1</sub> and S<sub>3</sub> treatments, probably because the number of grains was reduced so much that the demand for assimilate could be met by postanthesis photosynthesis. Notwithstanding that, the contributions of preanthesis assimilates to grain growth shown here seem to be higher than those commonly found (Bidinger *et al.* 1977), similar values have been found by other workers in small-grained crops (Gallagher *et al.* 1976; Austin *et al.* 1980; Siddique *et al.* 1989) and sunflowers (Hall *et al.* 1989). The estimated contributions of preanthesis assimilates to grain yield were strongly correlated with losses in stem dry weight between anthesis and maturity (Fig. 3a), indicating that much of the relocated assimilate came from the stems rather than from other organs.

All shading treatments decreased the demand in preanthesis assimilates by decreasing the number of grains. Therefore, the greater the sink-source relationship, the greater the stem dry weight loss (Fig. 3b). Because the removal of photoassimilates must have an upper limit, it can be suggested that

further increases in grain yield of this cultivar should be made from similar increases in source and sink strength because values for the contribution of preanthesis assimilates observed for the control treatment were high. In addition, retrospective analyses of the genetic improvement effects have shown that, while number of grains/m<sup>2</sup> increased, the total dry weight at anthesis remained unchanged both in Argentina (Slafer *et al.* 1990) and in Australia (Siddique *et al.* 1989). We are aware that the method we used to estimate the contribution of preanthesis assimilates to grain yield does not include dry matter losses through tissue senescence and respiration (Austin *et al.* 1980; Hall *et al.* 1989). Austin *et al.* (1977) calculated that 73% vegetative dry matter lost was allocated to grains. Applying this factor to correct our data indicates that the contribution of preanthesis assimilates to developing grains in the control treatment was 36% in 1987 and 26% in 1988. These values are still high.

Thorne & Wood (1988) suggested that, because of their position in the canopy, tillers are often shaded by taller shoots, and tillers might, therefore, be expected to be more affected by shading than the main shoots. However, we found no differences in the responses of different shoot categories to shading. Wall (1979) also found that reductions in grain yield and number of grains caused by shading were the same for the largest ears of the crop (presumably main-shoot ears) as in the smallest. Many workers have observed the strong positive correlation between number of grains and ear dry weight at anthesis (Wall 1979; Fischer & Stockman 1980; Stockman *et al.* 1983; Fischer 1985; Thorne & Wood 1987; Slafer *et al.* 1990). In this study, the correlation was present and was not altered by the inclusion of tillers and main-stem shoot values. This indicates that, although shading decreased ear dry weight of both categories at anthesis, it did not alter the number of grains produced per unit of ear dry weight by each category (Fig. 1b).

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## REFERENCES

- AUSTIN, R. B., EDRIKH, J. A., FORD, M. A. & BLACKWELL, R. D. (1977). The fate of the dry matter, carbohydrates and <sup>14</sup>C lost from leaves and stems of wheat during grain filling. *Annals of Botany* **41**, 1309–1321.
- AUSTIN, R. B., MORGAN, C. L., FORD, M. A. & BLACKWELL, R. D. (1980). Contributions to grain yield from preanthesis assimilation in tall and dwarf barley phenotypes in two contrasting seasons. *Annals of Botany* **45**, 309–319.
- BIDINGER, F., MUSGRAVE, R. B. & FISCHER, R. A. (1977). Contribution of stored preanthesis assimilate to grain yield in wheat and barley. *Nature* **270**, 431–433.
- CASAL, J. J. (1988). Light quality effects on the appearance of tillers of different order in wheat (*Triticum aestivum*). *Annals of Applied Biology* **112**, 167–173.

- COALDRAKE, P. D. & PEARSON, C. J. (1985). Development and dry weight accumulation in pearl millet as affected by nitrogen supply. *Field Crops Research* **11**, 171–184.
- FISCHER, R. A. (1975). Yield potential in a dwarf spring wheat and the effect of shading. *Crop Science* **15**, 607–613.
- FISCHER, R. A. (1985). Number of kernels in wheat crops and the influence of solar radiation and temperature. *Journal of Agricultural Science, Cambridge* **105**, 447–461.
- FISCHER, R. A. & AGUILAR, M. (1976). Yield potential in a dwarf spring wheat and the effect of carbon dioxide fertilization. *Agronomy Journal* **68**, 749–755.
- FISCHER, R. A. & STOCKMAN, Y. M. (1980). Kernel number per spike in wheat: responses to preanthesis shading. *Australian Journal of Plant Physiology* **7**, 169–180.
- GALLAGHER, J. N., BISCOE, P. V. & SCOTT, R. K. (1975). Barley and its environment v. stability of grain weight. *Journal of Applied Ecology* **12**, 319–336.
- GALLAGHER, J. N., BISCOE, P. V. & HUMBER, B. (1976). Effects of drought on grain growth. *Nature* **264**, 541–542.
- GALLAGHER, J. N. & BISCOE, P. V. (1978). Radiation absorption, growth and yield of cereals. *Journal of Agricultural Science, Cambridge* **91**, 47–68.
- HALL, A. J., CONNOR, D. J. & WHITFIELD, D. M. (1989). Contribution of preanthesis assimilates to grain filling in irrigated and water stressed sunflower crops. I. Estimates using labelled carbon. *Field Crops Research* **20**, 95–112.
- HOWELL, T. A., MEEK, D. W. & HATFIELD, J. L. (1983). Relationship of photosynthetically active radiation to short wave radiation in the San Joaquin Valley. *Agricultural Meteorology* **28**, 157–175.
- JENNER, C. F. (1979). Grain filling in wheat plants shaded for brief periods after anthesis. *Australian Journal of Plant Physiology* **6**, 629–641.
- KIRBY, E. J. M. (1988). Analysis of leaf, stem and ear growth in wheat from terminal spikelet stage to anthesis. *Field Crops Research* **18**, 127–140.
- SIDDIQUE, K. H. M., BELFORD, R. K., PERRY, M. W. & TENNANT, D. (1989). Growth, development and light interception of old and modern wheat cultivars in a Mediterranean-type environment. *Australian Journal of Agricultural Research* **40**, 473–487.
- SLAFER, G. A. & ANDRADE, F. H. (1989). Genetic improvement in bread wheat (*Triticum aestivum* L.) yield in Argentina. *Field Crops Research* **21**, 289–296.
- SLAFER, G. A., ANDRADE, F. H. & SATORRE, E. H. (1990). Genetic-improvement effects on preanthesis physiological attributes related to wheat grain-yield. *Field Crops Research* **23**, 255–263.
- STOCKMAN, Y. M., FISCHER, R. A. & BRITAIN, E. G. (1983). Assimilate supply and floret development within the spike of wheat. *Australian Journal of Plant Physiology* **10**, 585–594.
- THORNE, G. N. & WOOD, D. W. (1987). Effects of radiation and temperature on tiller survival, grain number and grain yield in winter wheat. *Annals of Botany* **59**, 413–426.
- THORNE, G. N. & WOOD, D. W. (1988). Contributions of shoot categories to growth and yield of winter wheat. *Journal of Agricultural Science, Cambridge* **111**, 285–294.
- TOTTMAN, D. R. (1987). The decimal code for the growth stages of cereals, with illustrations. *Annals of Applied Biology* **110**, 441–454.
- WARDLAW, I. F. (1970). The early stages of grain development in wheat: response to light and temperature in a single variety. *Australian Journal of Biological Science* **23**, 765–774.
- WALL, P. C. (1979). *An analysis of factors limiting grain numbers and yield of spring wheat in a low-latitude environment*. PhD thesis, University of Reading.