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Yield potential in a dwarf spring wheat and response to crop thinning

By R. A. FISCHER* and D. R. LAING†

International Maize and Wheat Improvement Centre (CIMMYT), Londres 40, Mexico 6, D.F.

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SUMMARY

Experiments with wheat describing the effects of crop thinning on grain yield and its components are presented. These were carried out over 5 years in northwest Mexico, using a high-yielding dwarf spring-wheat variety (*Triticum aestivum* cv. 'Yecora 70') grown under irrigation and high fertility. It was shown that thinning largely relieved competition for light, thus increasing photosynthate levels in the plants remaining after thinning. The objective was to evaluate this simple technique as a guide to understanding when grain yield and its components were determined and, in particular, the extent to which post-anthesis photosynthate supply limited yield.

There were major responses in grain yield with thinning between about 50 and 100 days after seeding, and in number of spikes and of grains with thinning between 50 and 90 days (50 % anthesis was reached at 87 days). Number of spikelets per spike showed small responses to early thinning (before 50 days). Number of grains/spikelet and kernel weight showed positive responses to thinning between 65 and 90 days, and 90 and 115 days, respectively. These results agreed with adjacent shading and CO_2 fertilization studies but, because of certain difficulties in interpretation of responses, pre-anthesis thinning was not considered a very useful technique.

Anthesis thinning was carried out on 21 separate crops: the kernel weight increase relative to the unthinned control ranged from 6 to 41 %, averaging 20 %. Anthesis thinning led to increases in stem weight during the first half of the grain filling period, followed by increases in grain growth rate in the latter half. The increase in final kernel weight was greater with higher temperature and lower radiation during grain filling; these variables explained 64 % of the variation in kernel weight response. It is suggested that the kernel weight response does indicate the degree of photosynthate limitation during grain filling, showing reasonable agreement with adjacent shading and CO_2 fertilization studies. It was concluded that anthesis thinning, because of its relative simplicity, is a useful technique. Implications for yield improvement in Yecora of the results provided by this technique are discussed.

INTRODUCTION

This paper continues a series dealing with limitations to grain yield potential in a high-yielding dwarf spring wheat grown under irrigation and optimal agronomic practices in north-west Mexico. Shading treatments have been used to examine the sensitivity of grain yield and its components to reduced light and lowered crop photosynthesis at different stages (Fischer, 1975). However, the results obtained cannot be extrapolated with complete certainty to predict the effects of increases in light and crop photosynthesis. Crop fertilization with carbon dioxide increased crop photosynthesis leading to increases in grain yield at certain stages (R. A. Fischer and I. Aguilar, unpublished data) but the technique requires substantial resources.

Under conditions of frequent irrigation and heavy fertilization, competition within the crop should largely be above ground and for light. Calculations of CO_2 gradients in crops (Allen, Desjardins & Lemon, 1974) have indicated that competition for CO_2 within the canopy is unlikely. Thus thinning treatments which remove plants from the crop will

* Present address: CSIRO Division of Plant Industry, P.O. Box 1600, Canberra City, A.C.T. 2601, Australia.

† Present address: Centro Internacional de Agricultura Tropical (C.I.A.T.), Apdo. Nal. 737, Cali, Colombia.

relieve competition for light. They can be used to examine responses to increases in light and presumably photosynthesis of the plants remaining after thinning (Puckridge, 1968; Willey & Holliday, 1971). This technique has the advantage of being relatively simple.

Thinning treatments were applied to the wheat crop at different stages of development in several experiments reported here. Subsequent effects on grain yield and numerical components of grain yield should indicate when and to what extent these are limited by competition for light in the crop situation. Particular emphasis was placed on thinning applied at the beginning of grain filling in order to see the degree to which light supply and photosynthate production during this period limited kernel weight and grain yield.

MATERIALS AND METHODS

Experiments spanned five winter cropping seasons from 1970 to 1975 at the CIANO Experiment Station (Centro de Investigaciones Agricolas del Noroeste) of the Instituto Nacional de Investigaciones Agricolas and located in northwest Mexico (latitude 27° N, altitude 40 m). One dwarf spring wheat cultivar (Yecora 70) was used throughout. Experiments were grown under high fertility, irrigation and optimal management: seeding densities were between 100 and 120 kg/ha, giving approximately 200 plants/m². Leaf rust (*Puccinia recondita*) was controlled by applications of Indar (Rohm and Haas). Other cultural techniques were described earlier as were weather details for 1970–4 (Fischer *et al.* 1976). Weather for 1974–5 and long-term data are presented in Table 1. Although year to year variations in temperature and radiation appeared to be small, they were sufficient to influence the crop considerably. In particular, 1972–3 and 1974–5 were cooler than average and 1971–2 warmer than average.

Table 1. *Weather data for the winter cropping season* 1974–1975 *and long-term means at CIANO, Mexico*†

Month	1974–75 T	1974–75 R	Long-term T	Long-term R
November	19·6	316	20·3	343
December	14·4	219	16·3	288
January	14·4	313	14·9	312
February	14·7	405	15·7	399
March	16·7	495	17·6	512
April	17·7	557	20·8	594
May‡	21·2	620	24·1	615

† T = monthly mean temperature (°C), R = monthly mean radiation, ly/day.

‡ 1974–5 data for 1–15 May.

Experiments reported here are described in Table 2. Some experiments included various genotypes but only data for Yecora 70 are presented. All experiments except Expts 73B, 74B and 75B were seeded between 28 November and 9 December of the year previous to that shown in Table 2. Expts 73B, 74B and 75B each involved several seeding dates covering the interval late October to mid-January. Control (unthinned) grain yields were very high in 1971, 1974 and especially 1975; yields were somewhat lower in 1972 and 1973 (Table 2). With one exception, there was no significant agronomic or pathological limitation in these experiments, hence these yields were close to the genetic potential of the variety in each particular season. The exception refers to one seeding date of Expt 74B and will be mentioned later.

Experiments employed three or four replicates in a randomized block design, except where they involved various seeding dates. In the latter case a split plot design with seeding date as the main plot was used. Plots consisted of nine rows 20 cm apart, several metres in length, and oriented north–south. Thinning 50 % involved uprooting of the plants in every alternate row. Thinning 75 % removed, in addition, every alternate 25 cm segment of the rows remaining after 50 % thinning; these plants were cut off at ground level. Extreme thinning left either one row (the middle one) or two rows (third and seventh) completely intact while removing all other rows in the original nine-row plot; with the exception of Expt 73A, plants were also uprooted.

Table 2. *Thinning experiments*, 1970–1975

Year	Experiment	Control grain yield (t/ha†)	Thinning treatments
1971	71A	8·4	50 %, 75 % at anthesis‡
	71B	7·6	Extreme at anthesis
1972	72A	7·0	50 % every 14 days
	72B	6·0	Extreme at anthesis
	72C	6·6	Extreme at anthesis
1973	73A	6·8	Extreme at anthesis
	73B	5·5–8·1	Extreme at anthesis
	73C	7·6	50 %, extreme at anthesis
1974	74A	7·9	Extreme every 7 days
	74B	6·0–8·2	Extreme at anthesis
	74C	8·5	Extreme at anthesis
1975	75A	9·0	Extreme at anthesis
	75B	7·6–10·0	Extreme at anthesis

† Yield of unthinned control plots at 14 % moisture.

‡ Anthesis = 50 % of spikes with at least one dehisced anther.

In 73A, four extreme thinning treatments examined whether thinnning was relieved above ground competition (for light), or both above and below ground competition, the latter for either water or nutrients. The middle row of each plot was exposed by the following treatments applied to the neighbouring rows on each side:

(i) Cut neighbouring rows at ground level.

(ii) Push aside neighbouring rows so that middle row is unshaded.

(iii) Treatment (i) plus hessian side shades applied to middle row in order to simulate crop light environment.

(iv) Treatment (ii) plus similar shades as in (iii). Plants cut off at ground level at anthesis did not regrow and it is assumed that this treatment eliminated both above- and below-ground competition from neighbouring rows. On the other hand, the rows which were pushed aside remained green and active throughout grain filling and it was assumed that in this situation only above-ground competition had been reduced. Thus subtracting (ii) from (i) or (iv) from (iii) ought to measure the effect, if any, of below ground competition.

Measurements were made only at maturity, when plots were sampled by cutting at ground level. Usually the area sampled was greater than either 1 m², or 1 m of row in thec ase of thinned or partially thinned plots. Grain dry weight, numbers of spikes and spikelets, and kernel weight were measured; other numerical components of yield were calculated. Total dry weight was often also measured. All weights refer to samples dried to constant weight at 70 °C. On some occasions thinning at or after anthesis stimulated the production in the remaining plants of new tillers which produced small late spikes; these were excluded from all measurements taken.

RESULTS

Nature of competition

In Expt 73A (Table 3) there was a small but significant increase in yield and grain size when the crop was thinned at anthesis. Also the mean of the difference between treatment (i) and (ii), and (iii) and (iv) is close to zero for grain yield and equal to zero for kernel weight. This suggests that below ground competition was negligible. The fact that applying a hessian side shade in treatment (iii) brings the thinned crop yield and kernel weight back to values close to those of the unthinned control is additional evidence pointing to the dominance of above ground competition.

Table 3. *Effect of different extreme thinning treatments applied at anthesis (see text); Expt 73A*

Treatment	Grain dry weight g/m²	Grain dry weight %	Number of grains (100/m²)	Kernel weight (mg)
Unthinned	588	100	129	45·6
Thinned				
(i)	721	123	144	50·0
(ii)	666	113	132	50·4
(iii)	536	91	122	43·9
(iv)	571	97	131	43·5
S.E.	47		8	0·9

Thinning and stage of development

Thinning was carried out at regular time intervals in Expt 72A and 74A (Fig. 1); 50 % thinning was used in Expt 72A and extreme thinning in Expt 74A but in the latter case thinning treatments were not begun until 63 days after seeding.

For components expressed per unit length of

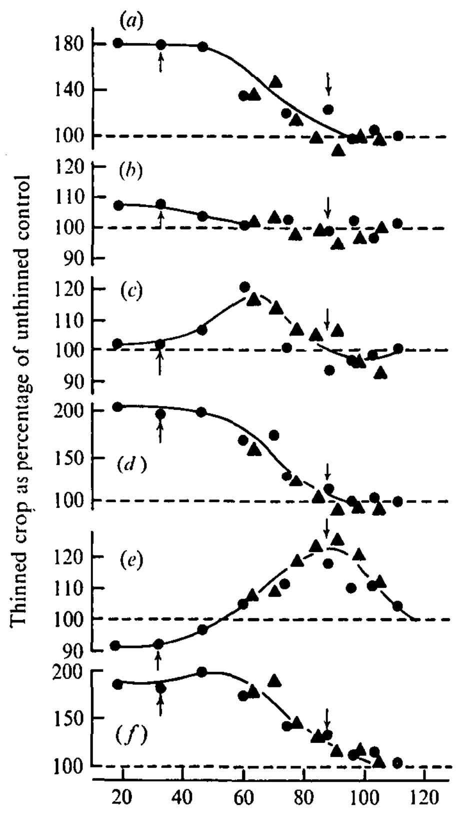

Fig. 1. Response of grain yield and its components to thinning at different times after seeding. (*a*) Number of spikes/m; (*b*) number of spikelets/spike; (*c*) number of grains/spikelet; (*d*) number of grains/m; (*e*) kernel weight; (*f*) grain weight/m. Expt 72A (circles) and Expt 74A (triangles). Up-directed arrow = mean date of floral initiation, down-directed = mean date of 50 % anthesis.

remaining row in Fig. 1 (number of spikes/m, number of grains/m, and grain weight/m) interpretation is relatively clear. Provided there is interrow light competition at the moment of thinning in the unthinned control crop, thinning means more light relative to the control for the remaining plants from that point in time onwards. Thus if one of the above components increases over the control value with thinning, then the component is sensitive to light competition in the control crop during some or all of the period after the particular date of thinning. With progressively earlier thinning in Expt 72A there was a date (about 50 days) before which thinning gave no further increase in these components. This means, in the control crop before this date, that either there was no interrow competition or that the components were not limited by such competition. The former possibility is unlikely since at 46 days in a row spacing × seeding density trial with Yecora 70 under similar conditions, plants in 20 cm rows were already 26 % lighter than those in 40 cm rows at the same plant density per meter of row.

It is concluded from Fig. 1 that in the control crop grain yield (grain weight) was sensitive to competition from about day 55 until day 100, and the number of spikes and grains sensitive from day 50 to day 90 (50 % anthesis occurred at day 87). With 50 % thinning before 50 days (Expt 72A), competition was relieved sooner, more growth and tillering presumably took place, but despite the thinning full light interception was still reached within 4 weeks. Apparently it was light interception after about 60 days that limited grain yield and numbers of spikes and grains in the unthinned crops, such that there was no additional advantage from the extra radiation received and extra growth associated with thinning before about 50 days. The extra tillering was probably balanced by higher tiller mortality (Fischer *et al.* 1976).

Had extreme thinning begun earlier in Expt 74A, there probably would have been extra responses to such thinning because the remaining plants with early extreme thinning would have always received more radiation than those of later thinned plots. That extreme thinning at and after 63 days gave results similar to 50 % thinning (Fig. 1) was likely due partly to the fact that in the latter case a high level of interrow light competition was never again achieved after thinning and partly to fortuitous seasonal weather differences (see later).

The responses of number of spikelets/spike, number of grains/spikelet and kernel weight in Fig. 1 are less easy to interpret because these may have been affected indirectly by thinning as a result of increases in earlier-formed yield components and hence greater subsequent intra-row and intraplant competition. This complication may not enter in the case of number of spikelets/spike because it showed a small but significant response only when the plants were thinned early. However, it probably explains the lack of response to early thinning in number of grains/spikelet and the negative response in kernel weight. In a trial adjacent to Expt 74A with Yecora 70 plants spaced 60 cm apart (practically zero interplant competition at all times from seeding) and in addition seeded as in the unthinned control plots of Expt 74A, the number of grains/spikelet was only 13 % higher and kernel weight was actually 16 % lower in the spaced situation. Because the plants' response to extra early light is always in terms of more spikes (and slightly more spikelets) it is impossible to say from Fig. 1 whether the number of grains/spikelet or kernel weight would be directly influenced by extra light at any stage earlier than that at which they show their maximum responses (around 65 and 90 days respectively). Nevertheless for the control crop situation it is reasonable to conclude that these components are not limited by competition occurring before these respective dates. More certain is the conclusion that the number of grains/spikelet is sensitive to competition from 65 to 90 days and kernel weight sensitive from 90 to 115 days.

Thinning at anthesis

Each year a number of thinning treatments were carried out at 50 % anthesis (Table 2). The effect on number of grains of such thinning was small: on the average ($n = 20$) the thinned crops had 8 % more grains. This must have been due to the corresponding increase in the number of spikes, as the number of grains per spikelet was unaffected by thinning with an average ($n = 10$) of 2·02 for thinned and 2·00 for unthinned (see also Fig. 1), and number of spikelets/spike could not have changed. Several of the earlier experiments involved 50 % thinning as well as extreme (or 75 %) thinning. It was apparent that the increase in kernel weight with thinning at anthesis was always slightly greater with extreme thinning than with 50 % thinning. As a percentage of the control, final kernel weight averaged 122 % with extreme thinning and 115 % with 50 % thinning ($n = 3$).

The time changes in grain and stem dry weight in the presence and absence of thinning at anthesis were followed by weekly sampling of random shoots in Expts 72B and 73A (Fig. 2). In Expt 72B thinning led to a rapid increase in stem weight relative to the control. This difference was greatest by 23 days after anthesis, following which it decreased somewhat. On the other hand grain weight per shoot was not obviously increased by thinning until about 23 days after anthesis and subsequently the differences between thinned and control increased. The differences in grain weight per spike were entirely due to differences in kernel weight which was 29% higher at maturity with thinning. In this experiment there was a slight tendency for the thinned crop to senesce later than the control. In Expt 73A, stem dry weight increases with thinning were somewhat greater than in Expt 72B, the differences, however, showing the same pattern of temporal changes. Again grain weight differences appeared at about 25 days after anthesis but they were always less in Expt 73A than in Expt 72B as final kernel weight was only increased 10% by thinning. Also in contrast to Expt 72B, the thinned plots clearly senesced ahead of the unthinned control, the period anthesis to maturity being reduced 6 days by thinning.

All thinning treatments applied at anthesis are presented in Table 4. The most precise comparison between control and thinned crops is that based upon kernel weight. Control kernel weight ranged from 33·1 to 46·2 mg, whereas kernel weights with thinning were close to 50 mg with the exception of the sowing on 27 December in Expt 74B. In the latter case, stripe rust (*Puccinia striformis*) developed

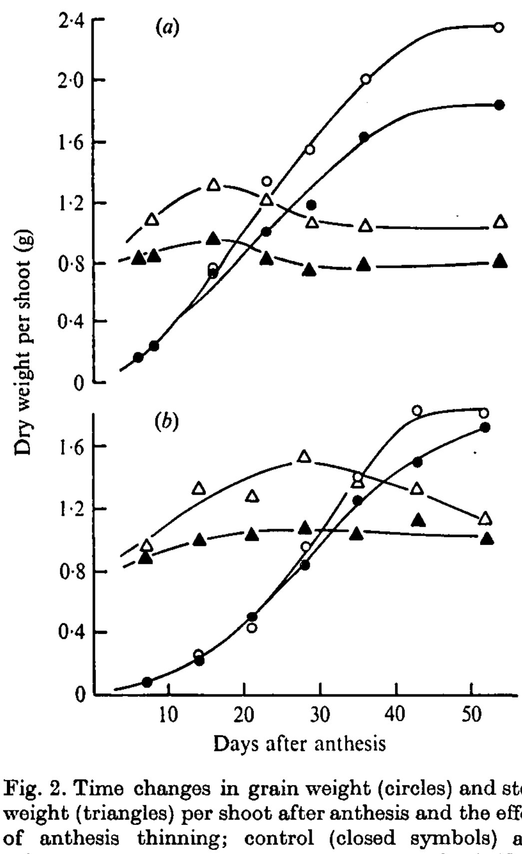

Fig. 2. Time changes in grain weight (circles) and stem weight (triangles) per shoot after anthesis and the effect of anthesis thinning; control (closed symbols) and thinned crops (open symbols). (*a*) Expt 72B; (*b*) Expt 73A.

to moderate levels after anthesis. The response in kernel weight to thinning ranged from 6 to 41%. An influence of year is seen when comparisons are made of crops seeded between 29 November and 9 December in each year. Thus the mean response was least in 1973 (12%); this was followed by 1975 (18%), 1974 (23%), 1972 (28%) and 1971 (32%). There also appeared to be a considerable effect of seeding date within years, but this effect shows no consistent trend between years.

Simple correlation coefficients were calculated relating the kernel weights for control and thinned crops and the percentage thinning response in Table 4 to various independent variables (Table 5). Weather variables were based on the period anthesis to maturity of the control crop. Since the major part of post-anthesis dry weight increase and the greatest post-anthesis inter-row competition occur in the first 25–30 days after anthesis, the weather variables were also calculated for this period, which was assumed to comprise the first 500 day degrees after anthesis. All Table 4 observations were used with the exception of those from the seeding on 27 December in Expt 74B, which was excluded because of disease. In control crops, kernel weight evidenced a strong negative relationship with temperature and a strong positive one with radiation input but when the crop was thinned, kernel weight showed a weak negative relationship with temperature. As a consequence of these relationships, the percentage response in kernel weight to thinning was associated positively with temperature and negatively with radiation input. There were no large differences between the two periods considered in Table 5. Also kernel weight and its response to thinning did not appear to be associated with the number of grains or with mean daily radiation.

DISCUSSION

It was assumed in the Introduction that below ground competition is negligible relative to competition for light and that the results can be interpreted in terms of increased photosynthesis as the direct result of thinning. Experiment 73A established the dominance of above-ground competition after anthesis; but it may be argued that substantial below-ground competition for nutrients or water could have taken place before anthesis. Since nitrogen is the only element for which fertilizer responses have been recorded at CIANO, it is likely that competition for nutrients would have been for nitrogen. In Expt 72A grain nitrogen content was determined; however, pre-anthesis thinning did not lead to a significant increase in grain nitrogen percentage, even when with later thinning grain yield per unit land area was reduced. On the other hand, in various experiments, grain nitrogen percentage was increased slightly but significantly with thinning at anthesis (+0·24 %, $n = 11$), although in Expt 73A the presence or absence of below-ground competition did not alter grain nitrogen. The increase in grain nitrogen percentage with anthesis thinning could be due to an earlier and more complete translocation of leaf nitrogen to the grain, more active root function and nitrogen absorption due to a greater surplus of photosynthate during grain filling, or finally, greater nitrate reduction associated with better illumination of green tissues. It is concluded nevertheless that competition for soil

Table 4. *Control crop variables and the effect of extreme thinning at anthesis on kernel weight (all experiments)*

Expt	Date: Sown	Date: Anthesis	Control: Grain dry weight (g/m^2)	Control: Number of grains ($100/m^2$)	Control: Kernel weight (mg)	Thinning: Kernel weight (mg)	Thinning: % increase over control: Mean	Thinning: % increase over control: S.E.
71A	8 Dec.	9 Mar.	720	188	38·3	47·7	24	2·2
71B	9 Dec.	9 Mar.	657	186	35·3	49·1	41	3·9
72A†	2 Dec.	29 Feb.	602	152	39·5	49·4	25	2·3
72B	3 Dec.	1 Mar.	517	135	38·6	49·7	29	2·9
72C	4 Dec.	29 Feb.	569	151	37·8	49·0	30	1·2
73A	6 Dec.	26 Feb.	588	129	45·6	50·2	10	1·9
73B	26 Oct.	5 Feb.	604	149	40·0	49·9	25	0·2
73B	16 Nov.	9 Feb.	469	120	39·3	47·9	22	1·5
73B	7 Dec.	5 Mar.	668	153	43·6	49·7	14	0·6
73B	27 Dec.	23 Mar.	695	160	43·6	49·5	15	1·9
73B	18 Jan.	6 Apr.	580	163	35·7	45·4	27	1·5
73C	9 Dec.	3 Mar.	651	141	46·2	51·2	13	1·2
74A	28 Nov.	22 Feb.	680	165	40·0	50·1	24	5·5
74B	15 Nov.	20 Feb.	707	161	42·5	53·4	26	5·6
74B	27 Dec.	18 Mar.	512	156	33·1	37·6	14	4·2
74C	1 Dec.	28 Feb.	729	173	42·4	50·9	20	2·0
75A	29 Nov.	8 Mar.	775	177	43·7	50·6	16	2·3
75B	1 Nov.	31 Jan.	654	143	45·6	48·6	6	2·4
75B	2 Dec.	7 Mar.	863	186	45·1	54·2	20	3·4
75B	31 Dec.	27 Mar.	826	194	42·8	51·7	21	4·3
75B	28 Jan.	16 Apr.	699	175	38·4	46·8	22	6·1

† From 50 % thinning; kernel weight adjusted up 7 %.

Table 5. *Simple correlation coefficients between kernel weight in control plots (KWC), kernel weight in thinned plots (KWT) and the kernel weight response to thinning expressed as a percentage (RESP), and several independent variables*

Independent variable†	Range	Dependent variable: KWC	Dependent variable: KWT	Dependent variable: RESP
GNO	12·0–19·4 × $10^3/m^2$	−0·16	0·18	0·30
AMRM	431–625 ly/day	−0·25	−0·30	0·16
AMTM	15·7–20·6 °C	−0·77***	−0·47**	0·66***
AMR	20·7–29·7 × 10^3 ly	0·64***	0·23	−0·61***
AMRG	1·2–2·3 ly/grain	0·44**	0·01	−0·53**
A5RM	383–627 ly/day	−0·31	−0·34	0·21
A5TM	14·7–20·0 °C	−0·80***	−0·41*	0·75***
A5R	11·5–17·3 × 10^3 ly	0·39*	0·01	−0·45**
A5RG	0·73–1·23 ly/grain	0·41*	−0·14	−0·57***

* $P < 0·1$; ** $P < 0·05$; *** $P < 0·01$.

† GNO = number of grains/m^2; AM prefix refers to anthesis to maturity, and A5 anthesis to 500 day degrees after anthesis; RM = mean daily radiation, TM = mean temperature, R = total radiation in period, and RG = total radiation per grain.

nitrogen was not a factor influencing the results presented here. It should be mentioned that the nitrogen fertilization used (200–300 kg N/ha) was always equal to or somewhat greater than that required for maximum grain yield.

Given the frequency of irrigation adopted, the likelihood of competition for soil water is remote. Some measurements of stem xylem pressure potential (Fischer, 1973) were made in mid-afternoon on 4 days during the grain filling period in Expt 73A. This is when evaporative conditions were greatest: nevertheless the thinned plants had a lower xylem potential (−14·3 bars) than the control ones (−12·7 bars), probably as a consequence of their greater exposure. Such differences are unlikely to have led to differences in stomatal closing. The fact that the duration of grain filling appeared to be either unaffected or hastened by thinning (see Fig. 2) also suggests that soil water competition was not being relieved by such thinning.

Thinning carried out at different dates throughout the crop cycle, although simple to execute, proved difficult to interpret. One reason was that competitive levels within the remaining rows and plants were changed as a result of the increased tillering and number of spikes caused by early thinning. It was difficult to quantify on the one hand the amount and period of the increase in light interception subsequent to thinning and on the other the number of organs (spikes, etc.) competing. For example, early 50 % thinning relieved competition only for as long as it took the crop to spread and fill in the space created by thinning. Such considerations have generally been ignored in thinning studies (Puckridge, 1968; Willey & Holliday, 1971; Green, Finkner & Duncan, 1971) but may affect their interpretation. For example, Watson & French (1961) concluded that because the grain-leaf ratio for wheat in rows spaced at 7 in. was no less than in 21 in. rows, there was no interrow competition in the former situation. These results could readily have been interpreted as showing an equal degree of mutual shading and light competition in both situations, the crop with 7 in. rows being no 'thicker' than the one with 21 in. rows by the time of anthesis because of increased pre-anthesis growth leading to more spikes per unit row length in the latter situation.

Thinning before anthesis

The results obtained here may not be comparable with other results because of the above-mentioned difficulties in interpretation. Also in the Puckridge (1968) study the control plant density was extremely high (1150/m^2) and in several other studies below ground competition was probably also operating (Watson, Thorne & French, 1962; Green *et al.* 1971). Despite this, the pattern of response of yield components to thinning seen here is similar to that reported by Green *et al.* (1971): major responses in number of spikes depending on thinning in the latter half of the pre-anthesis period plus minor responses in spike size. Puckridge (1968) showed up to a 60 % response in number of grains/spike, also dependent on thinning in the latter half of this period. In contrast Willey & Holliday (1971) found with thinning of crops having around 300 plants/m^2 that competition in the first half of the pre-anthesis period largely controlled the number of grains/spike. This became more marked at higher plant densities but was explained not because of direct effects on the developing spike but rather because of early competition limiting shoot size with subsequent limitations on spike size.

Puckridge (1968) and Green *et al.* (1971) observed a positive response in kernel weight which, although always small ($<$ 15 %), became larger the earlier the pre-anthesis thinning was carried out. This is evidence of direct effects on grain size of events before anthesis; neither here nor in the study of Willey & Holliday (1971) was such a response to thinning seen.

Of greater interest here is the general agreement regarding the determination of yield components between the thinning studies and adjacent shading, CO_2 fertilization and density studies with the same variety (Fischer, 1975; Fischer *et al.* 1976). In all studies photosynthate levels in the crops were being altered at different stages of development. The results may be summarized as follows, bearing in mind that 50 % anthesis was reached around 90 days:

(i) Early growth and tillering (before 50 days) was of little importance for yield, or even for determination of the number of spikes/m^2.

(ii) The number of spikes showed marked sensitivity to conditions from 50 until 90 days; since tillering ceases before 50 days, this sensitivity must reside in tiller survival.

(iii) The number of spikelets (fertile spikelets/spike) was relatively insensitive at all times.

(iv) The number of grains/spikelet showed moderate responses to changes in the crop during the period 60–90 days.

Of these components, the one showing the greatest positive response relative to the control, was clearly number of spikes (tiller survival) which was almost doubled with 50 % thinning. On the other hand, the shading studies suggest that the component most sensitive to reductions in light and photosynthate levels in the crop is the number of grains/spikelet.

Some implications of the above results for yield improvement in Yecora 70 and related genotypes has already been discussed (Fischer, 1975).

Thinning at and after anthesis

All studies already mentioned showed little or no effect of thinning at anthesis on number of grains. Thus discussion in this section is limited to direct effects on kernel weight. No such effects were seen by Puckridge (1968) and Willey & Holliday (1971); a slight increase in kernel weight (10 %) with one of the varieties used was found by Green *et al.* (1971). In marked contrast the data presented here showed kernel weight increases ranging from 6 to 41 % and averaging 20 % (see Table 4).

It was assumed that thinning at anthesis, by increasing the light intercepted by the remaining plants and thereby increasing photosynthate supply (source), should lead to an increase in kernel weight in situations where control kernel weight is limited by post-anthesis source. Photosynthetic area indices of the unthinned crops would have been around 7 at anthesis (Fischer, 1975), so that interrow light competition should have still been substantial. By measuring light at the soil surface immediately after 50 % thinning at anthesis in Expt 73C, it was estimated that interception by the mainly green tissue of the remaining plants increased 70 %; for extreme thinning this increase should have been considerably greater. Total dry weight and stem dry weight measurements (Fig. 2) in several experiments confirm that photosynthesis of the remaining plants increased; photosynthetic area measurements throughout grain filling in Expts 72B and 73A suggest that this was not due to increases in photosynthetic area duration. Similar increases in light interception and photosynthesis should also have occurred in the thinning studies of other workers referred to earlier; only with widely spaced and/or poorly developed control crops could they have been avoided. One must conclude therefore that in their situations kernel weight was not limited by source and hence approached its maximum potential as governed by genotype and perhaps modified by pre-anthesis conditions. Low pre-anthesis radiation (Willey & Holliday, 1971) and/or extremely heavy pre-anthesis competition (Puckridge, 1968) may have so restricted number of grains/m^2 and potential kernel size that post-anthesis photosynthate of the control crop was more than adequate to completely fill these kernels.

If the response of kernel weight to thinning at anthesis is a good index of the degree of source limitation during grain filling, this response ought to be related to factors affecting photosynthate supply during grain filling. Multiple regression analysis using the stepwise technique of Draper & Smith (1966), and each respective dependent variable and all the various independent variables in Table 5, gave the following 'best fit' models with $P < 0{\cdot}1$ as the level of significance for the retention of independent variables:

$$\text{KWC} = 52{\cdot}3 - 1{\cdot}2\ \text{A5TM} + 0{\cdot}00042\ \text{AMR} \quad (R^2 = 0{\cdot}71),$$

$$\text{KWT} = 60{\cdot}6 - 6{\cdot}0\ \text{AMTM} \quad (R^2 = 0{\cdot}22),$$

$$\text{RESP} = -11{\cdot}3 + 3{\cdot}0\ \text{A5TM} - 0{\cdot}0014\ \text{A5R} \quad (R^2 = 0{\cdot}64).$$

That the kernel weight response to thinning at anthesis (RESP) was negatively related to grain filling radiation (AMR) agrees with the hypothesis that this response is a measure of the degree of source limitation for grain filling. However, the major independent variable in the model was mean temperature (A5TM), apparently because the kernel weight of thinned crops although falling with higher temperatures, did so less rapidly than that from control crops. As well as the small and possibly direct depressing effect of temperature on kernel weight seen in the thinned situation, there must have been an additional depressing effect in the control crops. This could be indirect, operating via reduced photosynthate supply, possibly as a result of greater respiratory losses or hastened senescence. The latter effect is seen in the duration of the period anthesis to maturity in the control crop which was negatively related to the mean temperature ($r^2 = 0{\cdot}80$), being reduced from 54 to 35 days as temperature increased over the range shown in Table 5. A tendency for increased temperature to increase the degree of source limitation would agree with the results of Spiertz (1974) and results from other field experiments with Yecora 70 when grain filling temperatures were artificially altered (R. A. Fischer and R. Maurer, unpublished).

The absence of an independent effect of number of grains or a dominant effect of radiation per grain in the first and third of the above models is surprising: the presence of more grains in the control crop should increase the competition between grains during grain filling and hence the response to crop thinning at anthesis. A significant inverse relationship between kernel weight and number of grains/m^2 has been observed each year for Yecora 70 crops reaching anthesis at approximately the same calendar date and subject to different pre-anthesis treatments leading to a wide range in number of grains/m^2 (Fischer, 1975). Perhaps the absence of an effect of number of grains here is due to the restricted range in number of grains in the data set of Table 5 (12000–19400/m^2).

An additional check on the usefulness of the kernel weight response as an indicator of source limitation is provided by comparison with the results of experiments with post-anthesis shading (Fischer, 1975) and CO_2 fertilization. All crops in Table 6 were seeded in the period 22 November to

9 December. The shading treatments involved approximately 50 % shading for the period anthesis to maturity. Carbon dioxide fertilization was carried out from 4 to 9 days after anthesis until maturity but only in 1971, 1972 and 1973. The source limitation factor refers to the ratio of the change with shading in final grain dry weight to that in total dry weight (Gifford, Bremner & Jones, 1973). All methods in Table 6 point to 1973 as a season when grain size was scarcely limited by post-anthesis photosynthate supply; reasons for this have been discussed in Fischer (1975). However, only the thinning results distinguish between the other four seasons. Part of the problem may be due to the failure to exactly standardize the shading technique in years before 1973 (Fischer, 1975). The narrow range of kernel weights for the thinned crops represented in Table 6 (48·4–52·4 mg) and the significant relationships found between the response to thinning and appropriate weather variables, suggests that the thinning data of Table 6 may be the best index of source limitation. It is interesting that a source limitation factor similar to that derived from dry-weight differences in the shading studies and calculated for crops thinned at anthesis, varied little (0·33–0·62) and showed no clear seasonal effect. Since these ratios were always less than one with both shading and thinning treatments, it appears that the stem generally buffered grain yield against the full effect of changes in photosynthate supply.

Thinning at anthesis indicated the maximum possible kernel weight achievable in the absence of post-anthesis photosynthate limitation. Comparing this kernel weight, which appeared to be relatively independent of environment as might have been expected, with the kernel weight in the unthinned crops indicates the maximum amount by which grain yield could be increased through increases in post-anthesis photosynthesis. Thinning increased crop photosynthesis in the first half of the grain-filling period (Fig. 2); grain growth, however, was increased in the latter half of this period probably because the extra photosynthate, after temporary storage in the stems, was translocated to the grains only after the potential grain growth rate began to exceed current photosynthesis. Genetic modifications so as to increase post-anthesis crop photosynthesis could follow this pattern; that is, increasing photosynthesis in the first half of the grain-filling period and taking advantage of temporary stem storage of excess photosynthate. Since there is almost full light interception in this period, increases in photosynthesis could only come from greater efficiencies per unit light intercepted by green tissue, whether it be lamina, sheath, peduncle or spike.

Table 6. *Various indices of the limitation to grain filling by photosynthate supply in five seasons (see text)*

Year	Shading: Reduction in kernel wt. (%)	Shading: Source limitation factor	CO_2 fertilization† (% increase in kernel wt.)	Thinning (% increase kernel wt.)
1971	18	0·74	13	32
1972	18	0·87	20	28
1973	2	0·41	5	12
1974	20	0·75	—	23
1975	20	0·71	—	18

† R. A. Fischer and I. Aguilar (unpublished data).

Alternatively, prolonging the duration of photosynthetic tissue in the latter half of the grain-filling period could, via increased light interception, increase photosynthesis then; greater grain growth rates related to greater current photosynthesis should result in this period. Nevertheless the thinning data suggest that a maximum average yield gain of only about 20 % could be achieved through such modifications alone. Also the increase in the post-anthesis photosynthate production by the whole crop required for a given increase in photosynthate ultimately reaching the grains may because of stem buffering have to exceed considerably this latter increase.

Comparison with thinning studies of other authors suggests that there are substantial genotypic differences in the response to thinning at anthesis: Yecora 70 appears to be more source-limited than other genotypes studied. Since thinning at anthesis is relatively easy to carry out and to interpret, at least under irrigated high-fertility conditions, it would appear very useful for comparing genotypes and perhaps indicating likely parental combinations for higher yield (for example crossing source-limited genotypes with source-unlimited ones). Such comparisons will be reported in a later paper. It should be emphasized here, however, that some attention needs to be paid to standardizing the thinning technique. The extreme thinning used here is considered the simplest and least time consuming. Plots should be seeded at the optimal rather than extreme densities, and rows should be narrowly spaced (20 cm or less seemed satisfactory), so that intra-row competition after thinning is lessened. If new tillers are produced in response to thinning at anthesis, these should be excluded from the maturity harvest.

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