Aust. J. Agric. Res., 1978, **29**, 443–58

Effect of Environment and Cultivar on Source Limitation to Grain Weight in Wheat

R. A. Fischer[AB] *and D. HilleRisLambers*[AC]

[A] International Maize and Wheat Improvement Centre, Londres 40, Mexico 6 DF.
[B] Present address: Division of Plant Industry, CSIRO, P.O. Box 1600, Canberra City, A.C.T. 2601.
[C] Present address: International Rice Research Institute, P.O. Box 2453, Bangkok, Thailand.

Abstract

The relative increase in final kernel weight (SR, %) with an artificial reduction of about 80% in the number of grains per spike was assumed to estimate the degree of post-anthesis assimilate or source limitation to grain weight in wheat. This assumption was supported by comparisons with other treatments designed to alter the ratio of source to grain number. SR was determined in crops grown under irrigation and high fertility in north-west Mexico over a 5 year period, in order to examine the effect of environment (year, sowing date) and cultivar on source limitation. Some old tall cultivars and many modern short cultivars of wheat (*Triticum aestivum* L., *T. turgidum* L.) and triticale (× *Tritosecale* Wittmack) were studied.

For modern cultivars, kernel weight always appeared to be limited by source, SR averaging 21% over all years for eight such cultivars. For a given cultivar, environmental effects were considerable, being partly explained by a positive relationship between SR and mean temperature after anthesis. Each year SR was significantly affected by cultivar and, despite cultivar by year interaction, showed some consistency between years. Old bread wheats and triticales usually showed low source limitation (SR < 10%), whereas most modern cultivars, regardless of species, showed higher source limitation (SR up to 50%) and higher grain yields, probably because of higher grain numbers per sq metre. Within this latter group, there was no relationship between SR and grain yield. The kernel weight attained as a result of grain number reduction, defined here as potential kernel weight, was a stable cultivar trait useful in understanding yield variation.

Introduction

The question has often been posed whether grain yield in cereal crops is more limited in the post-anthesis period by source, in other words the supply of assimilate to the growing grains, or by sink, namely, the capacity of the growing grains to accumulate available assimilate. While this question is probably an oversimplification, for simultaneous limitation by both source and sink has now been proposed (Bingham 1971), quantification of the degree to which grain weight is limited by post-anthesis source, and of the influence of environment and cultivar, would be useful. Environment does appear to influence source limitation in wheat (Fischer 1975; Fischer and Laing 1976), but information on cultivar effects is lacking. Such information could be of use in breeding for higher yields. For example, changes in source limitation as a result of past breeding progress may indicate future breeding directions.

The degree of source limitation will be sensitive to the amount of interplant competition and therefore, for greatest relevance, source limitations must be determined in crops growing in typical field situations. Also a simple rapid technique is required for its determination if many cultivars are to be studied. One such technique could be based on the kernel weight increase, observed by Konovalov (1966), Bingham

(1967, 1971) and others, with artificial reduction in the number of grains per spike at anthesis. Similarly the increase in kernel weight with crop thinning at anthesis (Fischer and Laing 1976) should be related to source limitation. This paper reports an investigation of the former technique, including its comparison with the latter, as means of providing a quantitative estimate of the degree of source limitation to grain weight in wheat. Environmental and cultivar effects on estimated source limitation in irrigated crops are reported, their causes examined, and their consequences for breeding discussed.

Materials and Methods

Theory

In irrigated wheat crops grain number, whether per unit area or per spike, appears to be largely determined by the time of anthesis and little influenced by such treatments as post-anthesis shading (Fischer 1975), or crop thinning (Fischer and Laing 1976) and flag leaf removal (R. A. Fischer, unpubl. data) applied at anthesis. The influence of post-anthesis source upon grain yield is therefore reflected in changes in kernel weight. To estimate this influence, we measured the response of kernel weight to artificial reduction at anthesis in the number of grains per spike.

Kernel weight usually increases with reduction in grain number per spike (Konovalov 1966; Bingham 1967; Walpole and Morgan 1973; Spiertz 1974), although Lupton and Ali (1966) reported kernel weight decreases. Decreases, albeit small, were only found with a few tall cultivars in our study. The kernel weight increase is asymptotically related to the number of grains removed (Bingham 1967; Fig. 1). We assume this reflects a diminishing response to an increasing assimilate supply to each grain remaining. We define potential kernel weight as the asymptote, or the kernel weight attained with unlimited assimilate supply. For practical purposes the potential kernel weight was assumed to be that given by a substantial reduction (*c.* 80%) in grain number per pike. Furthermore, we assume that limitation of kernel weight, and hence yield, by post-anthesis assimilate supply is estimated by the difference between potential kernel weight and control kernel weight (no grain number reduction). This difference, expressed as a percentage of the control kernel weight, is termed the degree of source limitation, abbreviated to SR. Potential kernel weight should be independent of factors affecting post-anthesis assimilate supply (barring drastic curtailment of grain filling), but may be affected directly by post-anthesis environment, as well as by pre-anthesis assimilate supply and environment, and most likely by cultivar also.

Data from the response of kernel weight to crop thinning at anthesis (Fischer and Laing 1976; R. A. Fischer, unpubl. data) were used wherever available as an independent check on estimates of the degree of source limitation given by SR. Nine-row plots were thinned to a single central row, and, because of the resultant substantial increase in light received by this remaining row, the kernel weight attained was assumed to estimate also potential kernel weight. With the kernel weight of unthinned plots as control, the degree of source limitation (abbreviated to ST) was calculated in the same manner as for SR. For further validation, these estimates were compared when possible to other indications of source limitation, namely, the kernel weight decrease (as a percentage of control) with post-anthesis shading (Fischer 1975) or with flag leaf (lamina only) removal at anthesis, and the kernel weight increase with post-anthesis carbon dioxide fertilization (Fischer and Aguilar 1976).

Experiments

All experiments were carried out during five successive winter cropping cycles at CIANO* (lat. 27° N., alt. 40 m) near Ciudad Obregon in north-west Mexico. The climate is characterized by mild dry winters with rapidly rising temperatures and radiation levels in the spring; weather conditions for the experimental years (1970–1975) are summarized elsewhere (Fischer 1975; Fischer and Laing 1976). Wheat was seeded in plots in November–December each year and in January also in some years. Seeding density was normal (about 100 kg/ha), fertility was high and crops were irrigated throughout. Where necessary with taller cultivars, lodging was prevented by growing crops through mesh. Disease and weeds were controlled and yields were generally high, ranging from 4 to 9 t/ha.

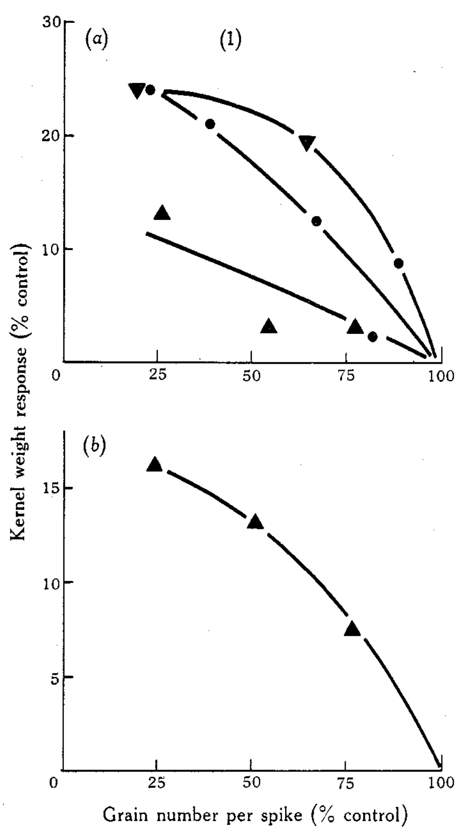
Each season SR was estimated in experiments which usually included cultivars from three species (bread wheat *Triticum aestivum* L., durum wheat *Triticum turgidum* L., and triticale × *Tritosecale* Wittmack). Cultivars studied ranged from tall traditional varieties of relatively low yield potential to dwarf ones of very high potential. Generally bread wheat cultivars predominated with Yecora 70, a high-yielding dwarf cultivar, serving as a standard in all experiments, and with eight modern dwarf cultivars common to all seasons. Thinning and shading treatments were applied to the eight common cultivars and various others in the same or immediately adjacent experiments. Carbon dioxide fertilization was given only to Yecora 70 in adjacent experiments.

Grain number reduction treatments were located at a sufficient distance from the plot boundary to avoid edge effects. Pairs of representative shoots, matched for spike size, height and anthesis date, were selected within as small as possible a region of the crop and treatments (control, grain number reduction) assigned in each pair at random. Pairs were replicated several times within the plot, and the plots themselves were usually replicated three or four times in randomized block or split plot designs depending on the experiment. The total number of pairs of shoots treated for any given situation (for example, cultivar or sowing date) fluctuated between 12 and 20. Spikes were harvested at maturity and threshed by hand. Grains were counted, oven-dried at 70°C and weighed.

Many aspects of the technique for reducing grain number were examined in preliminary experiments largely with the cultivar Yecora 70. Eliminating some grains from many spikelets produced the same results as eliminating all grains from some spikelets, so for simplicity the latter method was adopted. Grain elimination via removal of the ovary and/or very young grains with forceps gave kernel weight responses not significantly different from grain number reduction through cutting off whole spikelets with scissors. In the interests of rapidity, spikelet cutting was adopted as a standard technique. For substantial reduction in grain number (*c.* 80%), spikes were reduced to four spikelets, two on either side of the rachis and evenly distributed over the whole of the original spike (spikes normally had about 20 grain-bearing spikelets). The rachis was cut off above the uppermost remaining spikelet, and other spikelets to be removed were trimmed back to the rachis. Grain number at maturity in the four spikelets left was not significantly different from that in the corresponding spikelets of the intact control spike. Over many experiments with Yecora 70 and other cultivars, grains from the corresponding spikelets of the control spike averaged $4\cdot1 \pm 0\cdot5\%$ (± standard error of mean) heavier than the mean kernel weight of the

* Centro de Investigaciones Agricolas del Noroeste, Secretaria de Agricultura, Mexico.

whole control spike. This represents a minor error in the generally adopted method here of calculating SR by using the latter figure as the control kernel weight.



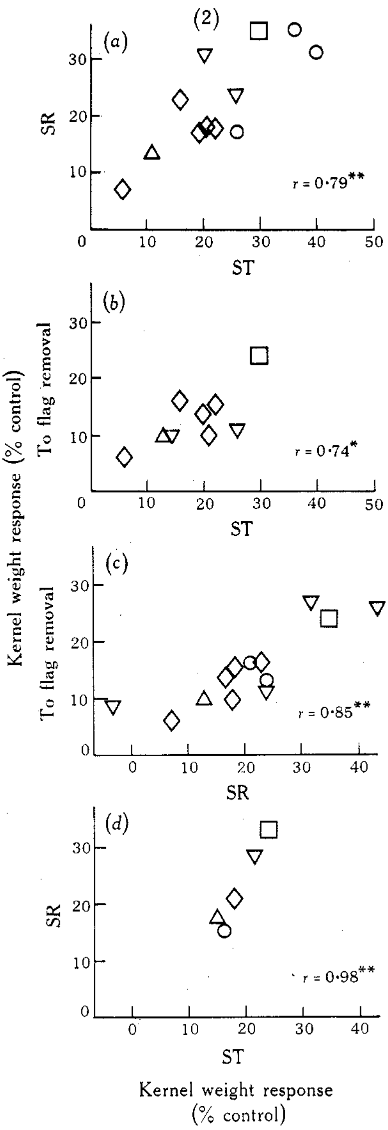


Fig. 1. Response of kernel weight (% control) to grain number per spike (% control) remaining after grain reduction: (*a*) Yecora 70 in 1971 (●), 1973 (▲) and 1974 (▼); (*b*) mean of 12 cultivars in 1973. Grain number variation as a result of differing degrees of grain number reduction at anthesis.

Fig. 2. Relationships between kernel weight responses to grain number reduction, flag removal and crop thinning at anthesis. Yecora 70 (*a*, *b*, *c*), and the yearly mean of eight cultivars (*d*); data from various experiments over 5 years: 1971 (○), 1972 (□), 1973 (△), 1974 (▽), and 1975 (◇).

Finally, studies revealed that SR was relatively insensitive to the exact timing with respect to anthesis (see Fig. 4) of the application of grain number reduction, to the exact location of the treated spikes in the canopy (upper or lower positions), and to whether grain number reduction was applied to one or all spikes of a given plant.

Results

Comparison of Techniques across Environments and Cultivars

In an experiment in 1974 when anthesis thinning and post-anthesis shading were used to give, along with an unmodified control crop, three post-anthesis crop environments supposedly varying in assimilate supply, SR varied in accord with the presumed variation in assimilate supply (Table 1). When in addition the flag leaf lamina of some shoots in each environment was removed at anthesis, SR for these shoots increased in the control and especially in shaded situations, as would be expected from considerations of assimilate supply (Table 1). Potential kernel weight estimated by grain

Table 1. Effect of shoot treatment at anthesis on kernel weight under three post-anthesis environments

Yecora 70, 1973–74 (sown 15 November); shading intensity 50%

Shoot treatment	Kernel weight (mg) Unmodified crop	Thinned crop	Shaded crop
No flag leaf removal			
Control	44·7	57·6	38·7
Grain reduction	55·5	55·7	55·8
(SR)	24%	−3%	44%
Flag leaf removal			
Control	39·7	52·7	28·5
Grain reduction	54·9	55·1	51·7
(SR)	38%	5%	81%

SEM, 1·1 mg; environment × treatment interaction highly significant.

reduction varied little (51·7–55·8, mean 54·8 mg) and was close to the mean potential kernel weight estimated by crop thinning (55·2 mg). ST for the unmodified crop was 29% (SR = 24%) in the absence of flag leaf removal, and 33% (SR = 38%) with flag leaf removal. The agreement between SR and ST is further illustrated by a 1974–75 experiment in which Yecora 70 was sown at four dates, every 28 days from November 1. The degrees of source limitation for the four respective crops were as follows: SR 7, 17, 18 and 18±2·7% *v.* ST 6, 20, 21 and 22±2·3%. Potential kernel weight averaged 51·3 mg with grain reduction and 50·4 mg with crop thinning.

All experiments in which comparisons can be made of environmental effects on the degree of source limitation, estimated by SR, ST and more approximately by the kernel weight response to flag leaf removal, are summarized in Fig. 2. Different environments resulted from year and seeding date variation, and from crop thinning and shading as in Table 1. All pairwise comparisons amongst the three techniques with Yecora 70 (Figs. 2*a*–*c*) resulted in statistically significant and fairly close relationships. The relationship between SR and ST improved when yearly averages of the eight common cultivars were used (Fig. 2*d*).

Table 2 summarizes the variation in SR, ST and kernel weight response to other treatments over the five years, with seeding date held constant within the optimal period for maximum yield. All techniques point to 1973 as the year when responses were smallest and, presumably, source limitation was least in the control crop situation. Differences between other years in responses were not clear-cut, although again there is good correspondence between SR and ST values.

Each year SR and ST were determined for a number of cultivars. There were generally significant cultivar effects on SR and ST, and a highly significant positive relationship ($r = 0 \cdot 83^{**}$) was found between cultivar means for SR and ST in 1971 when a large and diverse group of cultivars ($n = 36$) was examined. However, relationships, although always positive (r ranged from $0 \cdot 14$ to $0 \cdot 62$), were not significant in the other four years when smaller sets of less diverse cultivars (n ranged from 9 to 12) were tested. The average slope of these five relationships was equivalent to an 8% response with grain reduction for a 10% response with crop thinning, about half the slope seen in Fig. 2*d* for environmental effects. Errors in determining SR and ST were often high (see Table 3), and such errors may also explain why correlations between the techniques were poor in 1972–1975. Using the 5 year average of each of the eight cultivars common to all years gave an improved correlation ($r = 0 \cdot 80^{*}$).

Table 2. Response of kernel weight (as percentage of control) to treatments designed to change the supply of assimilate during the post-anthesis period in each of five years

Yecora 70 and mean of eight modern short cultivars (for names see Table 4). All crops seeded late November–early December of preceding year

Variable	Year: 1971	1972	1973	1974	1975	SEM[A]
	Yecora 70					
Kernel weight response (%) to						
Grain reduction (SR)	24	35	13	27	20	5·0
Flag removal	13	24	10	11	15	2·8
Thinning (ST)	32	28	12	23	18	4·1
Shading	18	18	2	20	20	3·5
CO_2 fertilization	13	18	5	—	—	2·7
Grain yield (g/m^2)	688	563	636	704	819	31
	Mean of eight Cultivars					
Kernel weight response (%) to						
Grain reduction (SR)	15	34	18	29	21	2·0
Thinning (ST)	16	24	15	22	18	1·5
Grain yield (g/m^2)	623	517	613	649	738	11

[A] A pooled estimate based on data from all years.

A comparison across cultivars of SR and the kernel weight decrease with flag leaf removal is given by an experiment in 1974–75 comprising 48 diverse cultivars. The cultivar effect on the kernel weight decrease was statistically significant (cultivar means ranged from 0 to 23%), but it was only weakly correlated ($r = 0 \cdot 29^{*}$) with SR. This lack of close relationship may partly be explained by variation between cultivars in the ratio of the area of flag leaf to total green area per shoot; mean flag leaf lamina area ranged from 22 to 54 cm^2 across cultivars.

Table 3. The degree of source limitation (SR, ST) and grain yield and grain number for various groups of cultivars each year

Group[A]	Number of cultivars	SR (%)	ST (%)	Group mean Grain yield (g/m²)	Grain no. (100/m²)	Cultivar mean Range SR Min.	Max.
			1971				
Old BW	8	−2	7	501	141	−19	12
Old T	2	−9	11	418	107	−11	−7
Modern BW	23	10	15	589	160	−3	34
SEM[C]		5·6	4·6	27	7		
			1972				
Old BW	1	4	9	305	90	4	4
Modern BW	8	32	21	517	165	22	48
SEM		6·8	3·6	42	12		
			1973				
Old BW	1	10	13	379	109	10	10
Modern BW	11	15	16	611	153	8	31
SEM		4·2	2·8	40	10		
			1974				
Modern BW	12	26	21	665	178	8	43
Modern T	1	27	49	586	162	27	27
SEM		7·1	5·3	24	10		
			1975				
Old BW	3	3		552	131	−7	13
Modern BW	33	20	18[B]	703	184	−6	43
Modern D	8	19		775	166	3	36
Modern T	4	32		727	168	20	43
SEM		5·3	3·6	20	6		

[A] BW, bread wheat; D, durum; T, triticale. In all years except 1975, the modern BW group contained one or two D cultivars.
[B] Only 10 of the 33 cultivars subjected to crop thinning.
[C] Standard error of cultivar mean.

Table 4. Cultivars common to the five experimental years, their degree of source limitation (SR, ST), grain yield and yield components; mean 1971–75, in order of descending yield

Cultivar[A]	Source limitation SR (%)	ST (%)	Grain yield (g/m²)	Grain number (100/m²)	Kernel weight (mg)	Anthesis date (days)[B]	Potential kernel weight (mg)
Yecora 70	28	22	684	167	42	89	51
Cocorit 71	27	25	675	148	46	89	59
Cajeme 71	17	16	671	159	42	98	50
Siete Cerros 66	19	16	658	191	34	95	40
WW 15	23	14	632	185	34	98	40
Olesen	27	26	601	203	30	86	37
Sonora 64	13	13	563	151	38	79	45
Tobari 66	32	21	540	152	36	86	44
SEM	2·5	1·8	14	4	0·5		0·7

[A] All modern bread wheats, except Cocorit 71 which is a modern durum.
[B] Days from sowing.

Cultivar Effects on Source Limitation

Comparisons of all cultivars in each season showed significant or highly significant cultivar effects on SR and ST, with the exception of SR in 1973, and ST in 1973 and 1975 (Table 3). The biggest differences were seen in 1971 and 1975, when several old cultivars were included. These cultivars showed lower SR and ST values, and lower grain yields and grain numbers than modern short cultivars, although there was some group overlap in all variables (see also Fig. 3). It is not clear why SR values were universally low in 1971, leading to some negative values; despite this SR correlated well with ST as mentioned before, and a systematic operator error is suspected. Striking changes in triticales are evident in Table 3, with newer cultivars showing higher SR values than older ones. The absence of significant cultivar effects on SR and ST in 1973 is probably related to the weather of that year, which led to low grain numbers and generally low levels of source limitation (see also Table 2).

Table 5. Correlations between SR and ST, and grain yield and yield components across all cultivars each year; 1971, 1972 and 1975 experiments

Number of cultivars	Response used	Range of yield Min. (g/m^2)	Max. (g/m^2)	Correlation with source limitation Grain yield	Grain number	Kernel weight	Anthesis date
			1971				
33	Mean SR, ST	396	709	0·52**	0·23	0·15	−0·45*
23[A]	Mean SR, ST	487	709	0·42*	0·16	0·08	−0·28
			1972				
9	Mean SR, ST	305	569	0·61†	0·56	0·03	−0·51
			1975				
48	SR	466	860	0·26†	0·37**	−0·20	0·18
33[B]	SR	516	860	0·08	0·25	−0·27	0·26

† $P < 0{\cdot}10$. * $P < 0{\cdot}05$. ** $P < 0{\cdot}01$.
[A] Only modern bread wheat and durum cultivars of preceding line.
[B] Only modern bread wheat cultivars of preceding line.

SR and ST values for the eight cultivars common to all five years are shown in Table 4. Analysing these results across years and cultivars showed highly significant cultivar and cultivar × year effects, and significant year effects (year means were shown in Table 2). The variance components for SR and ST, respectively, were as follows: year (59, 17), cultivar (24, 14), year × cultivar (37, 25) and error (80, 41). Thus variance due to cultivar was smallest in both cases.

Possible relationships between the estimated degree of source limitation for cultivars shown in Table 3, and yield and yield components were examined by correlation analysis (Table 5). For a more precise estimate of source limitation the average of SR and ST was used wherever possible. Cultivar effects on yield and yield components were significant and usually large. When a number of old tall wheats were included in the correlation calculation (1971), there was a positive relationship between grain yield and source limitation (Table 5, Fig. 3*a*). When old wheats were excluded relationships with yield were weak (Table 5, Fig. 3*b*). Source limitation tended to show weak positive relationships with grain number per m^2, but no relationship with kernel weight or consistent relationship with anthesis date. Relationships for 1973 and 1974 (not shown in Table 5) were not significant, nor were those calculated from the 5 year averages for the eight common cultivars of Table 4.

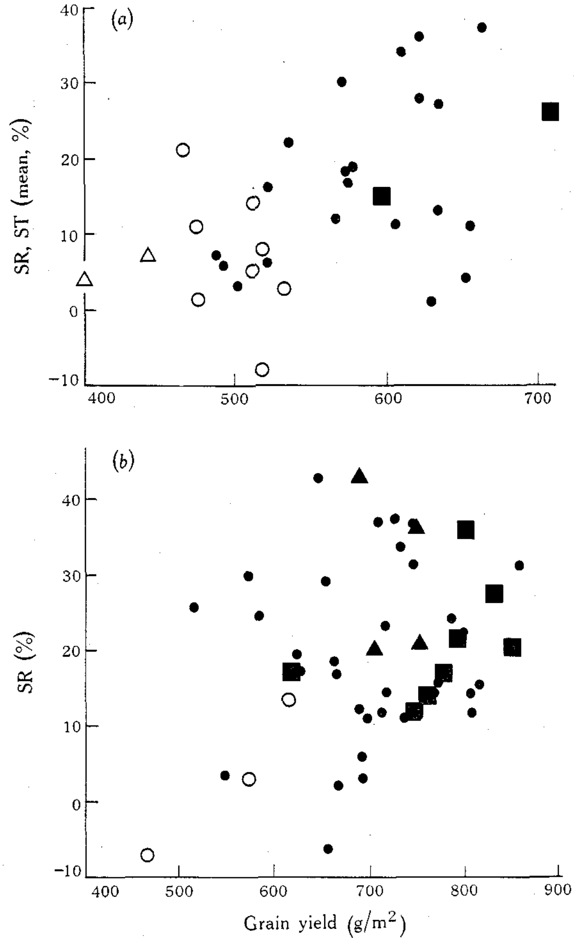


Fig. 3. Relationship between the degree of source limitation (SR, ST) and grain yield: (*a*) 1971; (*b*) 1975. Cultivar groups: old bread wheats (○), old triticales (△), modern bread wheats (●), modern durums (■), and modern triticales (▲).

The 1975 experiment provided the most extensive data on cultivar effects (highly significant) on potential kernel weight. The latter ranged from 35 mg (M Reo × No^2, a modern bread wheat with branched spikes) to 67 mg (Mexicali 75, a modern durum variety); the average values for the cultivar groups were 43 mg (old bread wheats), 47 mg (modern bread wheats), 59 mg (modern durums) and 58 mg (modern triticales). In the same experiment, potential kernel weight bore no relationship to the duration of the periods sowing to anthesis, or anthesis to maturity. Other correlations with potential kernel weight in 1975 were as follows:

	All cvv.	Modern bread wheats
v. grain yield	0·36*	0·03
v. grain number/m^2	−0·28†	−0·34†
v. kernel weight	0·72**	0·55**

† $P < 0·10$. * $P < 0·05$. ** $P < 0·01$.

Discussion

Technique and Assumptions

Changes in the post-anthesis assimilate supply as a result of shading, crop thinning and flag leaf removal led to changes in SR (e.g. Table 1) in the direction to be expected if SR was, as assumed here, measuring source limitation to kernel weight. Others have also shown the kernel weight response to grain number reduction to increase with shading (Stoy 1965), and with both shading and defoliation (Konovalov 1966).

The close association between SR, ST and the kernel weight response to flag leaf removal in a given cultivar across environments (Fig. 2), also supports the theory outlined earlier. The kernel weight increase with crop thinning (ST) demands that assimilate importation by the spike increases by about the same relative amount since grain number per spike was unchanged. That this kernel weight increase was no less than with reduction in the grain number per spike (SR) suggests that the capacity of the shoot to translocate to the spike was not limiting in the thinned and hence also the control situation. It does not imply that translocation capacity in the rachilla of each spikelet was not limiting. Nevertheless, the fact that kernel weight responses were no greater with retention of some of the grains of each spikelet than with retention of whole spikelets (SR) suggests that rachilla limitation was unlikely.

One apparent weakness in the theory outlined has, however, become evident. It is widely accepted that for the first approximately one-third of the grain-filling period, dry matter accumulation by grains is less than current assimilation, and surplus carbohydrate accumulates in stems (Stoy 1965; Thorne 1974). Only in the latter half of grain filling is grain growth likely to exceed current assimilation, and this is when assimilate limitations on grain growth ought to be greatest. However, delaying grain number reduction or flag leaf removal until 20 days after anthesis (about half-way through the grain-filling period with kernel weight still less than 50% of its final value) almost eliminated kernel weight responses to the anticipated changes in assimilate supply (Fig. 4). Brocklehurst (1977) has recently published similar results pointing to early rather than late competition between grains. Supported by his counts of endosperm cell numbers in grains, he believes the supply of assimilate to developing grains during the cell division phase (first 15 days or so) regulates the size of the grain sink, as reflected in the endosperm cell number. Thus grain sink size would tend to match the likely subsequent assimilate supply, thereby favouring complete grain filling and plump grains. The importance here of these results is that both the early cell division and later cell expansion phases of grain filling could conceivably be responsive to assimilate supply and that final kernel weight could be reduced because of assimilate shortages in either one, or both, of these phases. Potential kernel weight as determined in our study should have reflected the saturation of the responses to assimilate supply in both these phases, since treatments were always carried out within a few days of anthesis. Treatments carried out half-way through grain filling could measure assimilate limitations to cell expansion which, notwithstanding Fig. 4 and Brocklehurst (1977), could in some situations be substantial (e.g. late stress leading to 'pinched grain').

It may be argued that the implied competition between grains is for factors other than assimilate. This argument would seem especially impelling during the early cell division phase when assimilate supply is greater than grain growth. However, surplus assimilate and sensitivity to assimilate supply are not incompatible; the latter simply implies assimilate concentrations below those necessary to saturate grain responses. Also, notwithstanding the fact that percentage grain nitrogen always increased with grain number reduction (Konovalov 1966; R. A. Fischer, unpubl. data), direct limitation of final kernel weight through competition for minerals would seem unlikely in view of the general lack of association between mineral nutrition or grain composition and kernel weight. Finally, limitation by the supply of minerals or internal growth factors such as hormones, in a manner operating independently of assimilate level, would seem inappropriate for an annual plant in which assimilate not finally incorporated into the seed is lost for ever.

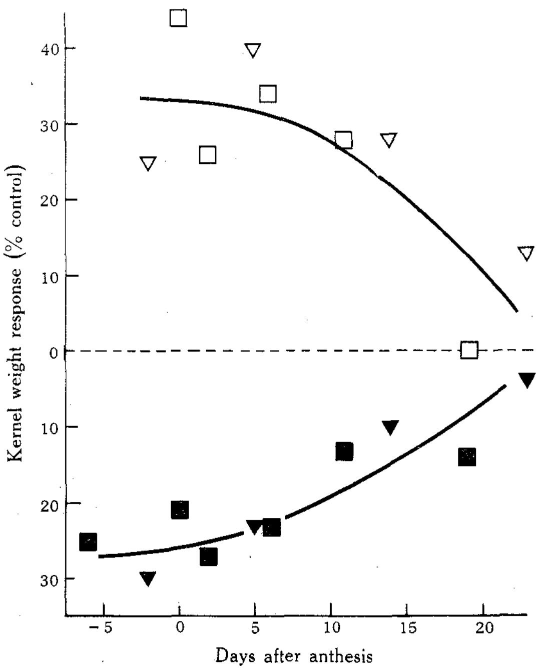


Fig. 4. Effect of timing of treatment upon the kernel weight response to grain number reduction (open symbols) and to flag removal (closed symbols). Yecora 70 in 1972 (□■) and 1974 (▽▼).

Environmental Effects on Source Limitation

Seasonal effects on SR and ST were substantial, and there was obviously no unique degree of source limitation for any given cultivar (Table 2). One might expect such effects on source limitation to be related to post-anthesis solar radiation and temperature, and to pre-anthesis environment as reflected in grain number per sq metre. For 21 crops of Yecora 70 grown over the 5 years, it has previously been shown that ST was positively related to mean temperature, but not related to mean daily solar radiation or to grain number (Fischer and Laing 1976). Across 13 Yecora 70 crops, SR ranged from 7 to 35% and was also positively related to mean post-anthesis temperature ($r = 0 \cdot 66^*$), which varied from 15·7° to 20·4°C, but unrelated to radiation (range 18·2–25·3 MJ/m^2/day) and grain number (range 14 100–19 400/m^2). The temperature effect (an increase in SR of 8% for each 1°C rise in temperature) suggests that the degree of source limitation increases as temperature increases; this would be expected and has been discussed elsewhere (Fischer and Laing 1976). The absence of a significant effect of solar radiation, even after taking the partial correlation with temperature constant, may reflect the small range in radiation values, since Table 1 shows that substantial artificial changes in grain-filling radiation did influence SR in the expected manner. The absence of an effect of grain number may also be due to the limited range in this variable. Fischer *et al.* (1977) showed at given temperature and radiation a consistent decline in kernel weight (and presumably increased SR) as the grain number in crops of Yecora 70 increased over the range 6000–30 000/m^2.

Potential kernel weight appeared to show small but significant variation between the above 13 crops of Yecora; it ranged from 48 to 57 mg (with grain reduction) and 47 to 54 mg (with thinning), the two determinations being closely correlated ($r = 0 \cdot 86^{**}$). The potential kernel weight, whether determined by grain reduction or thinning, bore no relationship to post-anthesis radiation and temperature, or the grain number/m^2, or the radiation and temperature in the 20 days preceding anthesis. When seven other crops, for which potential kernel weight was determined via thinning, were included in the analysis, there was a weak but significant negative relationship between potential kernel weight and the mean post-anthesis temperature ($r = 0 \cdot 47^{*}$, slope $= -0 \cdot 6$ mg/°C; Fischer and Laing 1976). Independent confirmation of the absence of an effect of pre-anthesis radiation was seen in 1972 when shading (65% intensity) of Yecora 70 from 28 to 8 days before anthesis reduced grain number to a very low level (4700/m^2, Fischer 1975); kernel weight rose to $51 \cdot 5 \pm 0 \cdot 6$ mg, the same as the potential kernel weight measured with grain reduction ($51 \cdot 2 \pm 0 \cdot 8$ mg) in an adjacent unshaded crop.

Yearly means for the eight common cultivars (Table 2) should give a more precise measure of seasonal effects: mean potential kernel weight each year ranged from 42 to 50 mg with grain reduction and from 41 to 47 mg with crop thinning. Values were again closely correlated with one another ($r = 0 \cdot 98^{**}$), which suggests significant seasonal effects, but associations with weather variables during grain filling or the 20 days prior to anthesis were not evident.

Although a large part of the apparently significant environmental variation in potential kernel weight remains unaccounted for, this variation, at least across the environments studied here, was small relative to the variation in control kernel weight. Also analysis of variance of the potential kernel weight data of the eight cultivars common to all five years showed that the year variance was only 9% of the cultivar variance, while the interaction variance was smaller still and non-significant. Thus we conclude that potential kernel weight is strongly controlled by cultivar, and it follows that the correlation between SR and temperature arose largely because increased temperature reduced the control kernel weight. Potential kernel weight can, however, be influenced by certain factors not operating in this study, such as posr-anthesis drought (Konovalov 1966), and heavy early attack by foliar disease (R. A. Fischer, unpubl. data).

Although yield always appeared to be limited to some extent by post-anthesis source (SR and ST averaged 21% for the five years and eight cultivars of Table 2), there was no association between seasonal effects on SR and ST, and those on grain yield (Tables 2 and 3). This is not surprising when it is considered that grain yield depends on the size of both the sink and the post-anthesis supply of assimilate, and not simply the balance between these components as indicated by the degree of source limitation. For example, the low yield of 1973 was associated with low grain numbers due to low pre-anthesis radiation (Fischer 1975), thus with a small sink, and with the smallest degree of source limitation in all five years studied On the other hand, 1972 showed low yield due especially to high post-anthesis temperature (Fischer *et al.* 1977), leading to the largest degree of source limitation measured.

Cultivar Effects

The effect of cultivar on source limitation, although smaller than that of environment and of cultivar by environment interaction, was significant. SR and ST values were consistently lowest (usually $<10\%$) for the old low-yielding bread wheats and triticales. Shorter modern wheats had higher yields associated with greater grain numbers, as has been seen in other studies (Aguilar and Fischer 1975). However, the generally greater degree of source limitation with such cultivars (SR and ST averaging 20%) was not entirely due to increased grain number, because potential kernel weight was also greater in modern compared with old cultivars, the increase being *c.* 11% and 46% for the bread wheats and triticales, respectively, of Table 3. The spectacular increase in the potential kernel weight of triticales is undoubtedly the result of recent selection directed specifically towards the elimination of grain shrivelling (Zillinsky 1974). There was no evidence that the higher source limitation of modern wheats was associated with a poorer total assimilate supply after anthesis. An exception to this were the two cultivars with the highest degree of source limitation in Table 4 (Olesen and Tobari 66); these are well known by wheat breeders as having rapid rates of leaf senescence (leaf firing) after anthesis.

Amongst the modern cultivars the associations of source limitation with grain yield, although tending to be positive, were small and non-significant. Extrapolating the trend seen by comparing old and modern wheats, we may have expected the highest yields to be associated with the highest SR values. Also when grain number was varied artificially in crops of Yecora 70 (Fischer *et al.* 1977), the highest yields were given by very high grain numbers leading to very small kernels (*c.* 30 mg), and judging by the potential kernel weight of Yecora 70 (51 mg, Table 4) a degree of source limitation well over 50%. The explanation of the lack of association of the highest yields with high SR values (e.g. in Fig. 3*b* when the most relevant set of modern cultivars was tested) may be that in crops not artificially manipulated as were the above Yecora 70 crops, there is a balance operating up to anthesis between, on the one hand, the maximization of sink size, and, on the other, the maximization of post-anthesis source. For example, it is probable that spike growth, which will influence grain number, competes for assimilate which could contribute directly or indirectly to the post-anthesis source. Other things being equal across cultivars, maximum yield may therefore be given more generally by a certain balance between sink and source developement, reflected in intermediate rather than extreme SR values. Also selection for plump grains and high hectolitre weight is not likely to favour genotypes with high SR values. All outstanding varieties released in north-west Mexico since 1970 (bread wheats Yecora 70, Cajeme 71, Jupateco 73 and Zaragoza 75, and durums Cororit 71 and Mexicali 75) showed SR values between 12 and 24% in the 1975 experiment.

The degree of source limitation determined under the favourable irrigated disease-free conditions of these experiments may be a guide to the sensitivity of cultivar yield to post-anthesis stress such as late drought or foliar disease attack. Yields should be less sensitive for cultivars with low source limitation. One test of this suggestion is provided for the eight modern cultivars of Table 4 by post-anthesis shading treatments which were carried out each year from 1972 to 1975 (R. A. Fischer, unpubl. data).

The mean grain yield reduction with 50% shading after anthesis ranged from 7% (Sonora 64) to 23% (Olesen), and was positively correlated ($r = 0{\cdot}83^*$) with the degree of source limitation (mean of SR and ST in Table 4). From this, one may also anticipate that old tall cultivars, with their consistently low degree of source limitation, are better buffered against post-anthesis assimilate shortage than are modern cultivars, a suggestion for which there is other supporting evidence (Evans and Wardlaw 1976).

As already mentioned, cultivar had a major effect on potential kernel weight. Also in the 1975 cultivar comparisons, the kernel weight of the bulk-harvested crop was related to potential kernel weight ($r = 0{\cdot}72^{**}$ all cultivars, $r = 0{\cdot}55^{**}$ short bread wheats), rather than to the adequacy of the post-anthesis supply of assimilate per grain, as estimated by SR ($r = -0{\cdot}19$ all cultivars, $r = -0{\cdot}27$ short bread wheats). Several experiments permitted a comparison between potential kernel weight and kernel weight under conditions when plants were widely spaced (>60 cm apart) from sowing. However, intraplant competition kept kernel weight in the latter situation relatively close to that obtained in the crop situation, and well below potential kernel weight in the case of most cultivars.

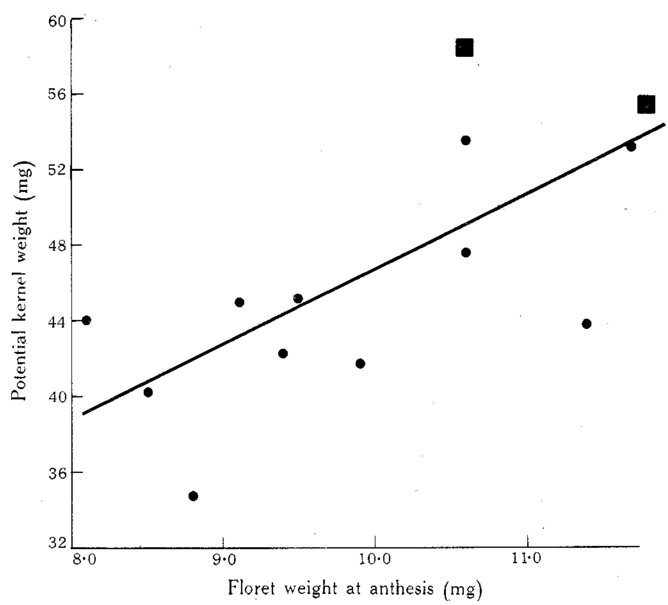


Fig. 5. Relationship between potential kernel weight (see text) and weight of spike tissue (including awns) per floret at anthesis; 11 modern bread wheats (●) and two modern durums (■) in 1974.

The cause of cultivar differences in potential kernel weight is not very clear, although the weak negative relationships shown in 1975 between potential kernel weight and grain number point to the possible influence of interfloret competition before anthesis. In the 1974 experiment, information was gathered at anthesis on the dry weight and floret number (all florets with plump green anthers) of typical spikes from crops of 11 modern bread wheats and two modern durums. The potential kernel weight of these cultivars, averaged for 1974 and 1975, was found to be significantly associated with the mean spike weight per floret. All cultivars were awned and including the awn weight in the spike weight gave the best relationship ($r = 0{\cdot}69^{**}$,

Fig. 5). This suggests that cultivars with large floral glumes, awns, and presumably carpels and ovaries, tended to have a greater potential kernel weight. The relationship of Fig. 5 was such that the potential kernel weight was about four times the original dry weight investment in floral parts.

The idea of a potential kernel weight largely controlled by cultivar facilitates the construction of a simple conceptual model of grain yield determination. Since grain number is largely determined at anthesis, it is possible to calculate, as suggested by Yoshida (1972), a potential yield at anthesis, which is the grain number multiplied by the potential kernel weight; this we term the potential sink for grain filling. The realized grain yield then becomes the result of the interaction of potential sink and post-anthesis assimilate supply or source, which is determined by various factors (solar radiation, leaf area and efficiency, etc.). Across the 48 cultivars of 1975, the association between grain yield and potential sink ($r = 0 \cdot 81^{**}$) was considerably stronger than that between grain yield and grain number ($r = 0 \cdot 64^{**}$). This difference was largely due to the inclusion of durum wheats and triticales with high yield derived from larger potential kernel weights but smaller grain numbers than bread wheats. For the bread wheat group alone both associations were strong ($r = 0 \cdot 79^{**}$ and $r = 0 \cdot 75^{**}$, respectively).

Whether information on source limitation will prove useful in plant breeding for higher yield is difficult to predict. The degree of source limitation for a cultivar does indicate the maximum amount by which its yield can be increased through improved post-anthesis source characteristics alone. Also, given cultivar differences in source limitation which are not connected to obvious deficiencies in source or sink, crosses between parents of high and low degrees of source limitation might be more likely to lead to physiologically complementary recombinants of higher yield than, for example, crosses amongst 'highs' or amongst 'lows'. Also it is possible that 'highs' exhibit some degree of grain shrivelling, their kernel weight being considerably less than potential, and this would have tended to militate against their retention in breeding programs despite their potential value as parents. Cultivar by environment interactions will be an obstacle in such work, but at least simple techniques for estimating source limitation are now available so that predictions can be tested.

Acknowledgments

The authors wish to acknowledge the ample provision of facilities and assistance by the Centro de Investigaciones Agricolas del Noroeste (CIANO) of the Mexican National Institute of Agricultural Research (INIA). One of us (R.A.F.) was supported by a Senior Research Fellowship of the Reserve Bank during the preparation of this paper.

References

Aguilar, I., and Fischer, R. A. (1975). Analisis de crecimiento y rendimiento de 30 genotipos de trigo bajo condiciones ambientales optimas de cultivo. *Agrociencia (Mexico)* **21**, 185–98.

Bingham, J. (1967). Investigations on the physiology of yield in winter wheat by comparisons of varieties and by artificial variation in grain number per ear. *J. Agric. Sci.* **68**, 411–22.

Bingham, J. (1971). Physiological objectives in breeding for grain yield in wheat. Proc. 6th Eucarpia Congress, Cambridge, pp. 15–29.

Brocklehurst, P. A. (1977). Factors controlling grain weight in wheat. *Nature (London)* **266**, 348–9.

Evans, L. T., and Wardlaw, I. F. (1976). Aspects of the comparative physiology of grain yield in cereals. *Adv. Agron.* **28**, 301–59.

Fischer, R. A. (1975). Yield potential in a dwarf spring wheat and the effect of shading. *Crop Sci.* **15**, 607–13.

Fischer, R. A., and Aguilar, M. I. (1976). Yield potential in a dwarf spring wheat and the effect of carbon dioxide fertilization. *Agron. J.* **68**, 749–52.

Fischer, R. A., and Laing, D. R. (1976). Yield potential in a dwarf spring wheat and response to crop thinning. *J. Agric. Sci.* **87**, 113–22.

Fischer, R. A., Aguilar, M. I., and Laing, D. R. (1977). Post-anthesis sink size in a high-yielding wheat: yield response to grain number. *Aust. J. Agric. Res.* **28**, 165–75.

Konovalov, Yu. B. (1966). Some consequences of restricting the number of ovaries in wheat and barley spikes. *Fisiol. Rast.* **13**, 135–43.

Lupton, F. G. H., and Ali, M. A. M. (1966). Studies on photosynthesis in the ear of wheat. *Ann. Appl. Biol.* **57**, 281–6.

Spiertz, J. H. J. (1974). Grain growth and distribution of dry matter in the wheat plant as influenced by temperature, light energy and ear size. *Neth. J. Agric. Sci.* **22**, 207–20.

Stoy, V. (1965). Photosynthesis, respiration, and carbohydrate accumulation in spring wheat in relation to yield. *Physiologia Plant. Supp. IV*, 1–125.

Thorne, G. N. (1974). The physiology of grain yield of wheat and barley. Rothamsted Exp. Stn. Rep. 1973, Part 2, pp. 5–25.

Walpole, P. R., and Morgan, D. G. (1973). The effects of floret sterilization on grain number and grain weight in wheat ears. *Ann. Bot.* **37**, 1041–48.

Yoshida, S. (1972). Physiological aspects of grain yield. *Annu. Rev. Plant Physiol.* **23**, 437–64.

Zillinsky, F. J. (1974). The triticale improvement program at CIMMYT. *In* 'Triticale', Proc. Int. Symp., El Batan, Mexico, Oct. 1973, Publ. Int. Dev. Res. Cent., Ottawa, pp. 81–5.

Manuscript received 9 February 1977