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Number of kernels in wheat crops and the influence of solar radiation and temperature

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SUMMARY

The number of kernels per m² (K) in well managed and watered wheat crops was studied using results of experiments in Mexico and Australia in which short spring wheat cultivars were subjected to independent variation in radiation, largely via artificial shading, and in temperature. Also crops subjected to differences in weather (year), sowing date and location within Mexico, revealed responses to the natural and simultaneous variation which occurs in radiation and temperature. Responses in K were interpreted in terms of spike dry weight at anthesis (g/m²) and number of kernels per unit of spike weight.

K was linearly and most closely related to incident solar radiation in the 30 days or so preceding anthesis, herein termed the spike growth period; for the cultivar Yecora 70 with full ground cover the slope was 19 kernels/MJ. This response seemed largely due to a linear response of crop growth rate to intercepted solar radiation. The proportion of dry weight increase partitioned to the spike increased somewhat with reduced radiation. Also increasing temperature in the range 14–22 °C during this period reduced K (slope approximately 4% per °C at 15 °C). The cause appeared to be lower spike dry weight due to accelerated development. The number of kernels per unit spike weight at anthesis was little affected by radiation or temperature, and averaged 78 ± 2/g for the cultivar Yecora 70.

With natural variation in radiation and temperature, K was closely and linearly correlated with the ratio of mean daily incident or intercepted radiation to mean temperature above 4·5 °C in the 30 days preceding anthesis. As this ratio, termed the photothermal quotient, increased from 0·5 to 2·0 MJ/m²/day/degree, K increased from 70 to $196 \times 10^2/\text{m}^2$. These responses of K to weather, sowing date and location were closely associated with variation in spike dry weight.

It was concluded that the ratio of solar radiation to temperature could be very useful for estimating K in wheat crop models. Also the analysis of K determination in terms of spike dry weight appeared promising, and suggests that wheat physiologists should place greater emphasis on the growth period immediately before anthesis.

INTRODUCTION

Much environmental variation in grain yield of wheat crops is associated with change in the number of kernels per unit land area. Under optimal conditions of soil and management, and excluding catastrophic meteorological events (e.g. frost at flowering), the variation in number of kernels which occurs must be related to the prevailing solar radiation, ambient temperature and daylength. The quantitative relationships with the first two of these variables are vital to understanding and modelling wheat yield, and are the subject of this paper.

The radiation and temperature regimes experienced by crops depend on location (climate), year and sowing date. Variation due to location (Table 1) and sowing date (Table 2) can be substantial, but that due to year (i.e. weather) is smaller (Table 2). Long-term monthly mean radiation and temperature tend to change in parallel seasonally (Table 2), while year-to-year deviations of radiation and temperature from their long-term means tend also to be positively correlated, except in winter months (Richardson, 1982).

Where data exist from a sufficient number of crops, the response to radiation and temperature

Table 1. *Approximate dates for floral initiation and anthesis and long-term climatic means for the initiation to anthesis interval in wheat crops sown at representative dates in various world locations*

Location*	Latitude	Approximate date		Total solar radiation (MJ/m²/day)	Daily mean temperature (° C)
		Initiation	Anthesis		
Kimberley R.S., Western Australia	15° S	Mid-June	End July	19·7	23·1
Clermont, Queensland	23° S	Mid-July	Early Sept.	17·7	15·9
New Delhi, India	28° N	Mid-Dec.	Early Mar.	16·8	14·2
Horsham, Victoria	37° S	Mid-July	Mid-Oct.	13·8	10·9
Pullman, Washington	47° N	Early Mar.	Early June	19·2	9·0
Swift Current, Canada	50° N	Mid-June	Mid-July	23·0	17·5
Rothamsted, U.K.	52° N	Early Apr.	Mid-June	14·5	10·0

* Extracted from Nix (1975) and referring to spring wheat, except for Pullman and Rothamsted which were estimated by the author and apply to winter wheat.

Table 2. *Average seasonal changes in total solar radiation and temperature at two wheat growing locations, CIANO (Mexico) and Rothamsted (U.K.)*

CIANO (latitude 27° N)*			Rothamsted (latitude 52° N)†		
Month	Mean solar radiation (MJ/m²/day)	Mean temperature (° C)	Month	Mean solar radiation (MJ/m²/day)	Mean temperature (° C)
Nov.	14·5	19·5	Mar.	7·6	5·5
Dec.	12·0	16·4	Apr.	11·6	7·4
Jan.	12·8	15·0	May	16·1	10·7
Feb.	16·7	15·8	June	17·3	13·8
Mar.	20·9	17·7	July	15·7	16·0
Apr.	24·4	20·1	Aug.	13·7	16·1
S.D. of monthly mean across years	1·0	1·2	—	1·9	1·3

* Period 1970–8. † Period 1972–9.

has been studied by various correlative techniques. With wheat this had generally revealed negative correlations of yield with temperature (Thompson, 1975; Desjardins & Ouellet, 1980; Michaels, 1981), but not always (Buck, 1961), and sometimes positive correlations with radiation or sunshine hours (Welbank, Witts & Thorne, 1968; Borojevic & Williams, 1982). However, in no study has variation in the number of kernels been examined explicitly. Also the covariance of radiation and temperature in the field limit this technique. To avoid the latter problem, some workers have independently manipulated the radiation or temperature regimes of field crops. Shading experiments with wheat have been common (Pendleton & Weibel, 1965; Welbank *et al.* 1968; Willey & Holliday, 1971; Fischer, 1975), and some deal explicitly with number of kernels, which is generally decreased by preanthesis shading. Temperature manipulation experiments have been less common (Peters *et al.* 1971; Fischer & Maurer, 1976) but confirm the adverse effect of increased temperature. Another approach has been the study of small areas of crop (mini crops) in controlled environments; this is difficult, and sufficient attention to exactly reproducing a crop-like community of wheat and appropriate amounts of radiation appears only to have been achieved by Evans (1978), who reported a positive association between number of kernels and radiation. Other controlled environment experiments studying the influence of radiation or temperature give results of limited quantitative value because of disparities in the competitive environment compared with field crops.

This paper develops quantitative relationships between number of kernels and radiation and temperature, using data collected largely by the author and colleagues over the last decade or so from irrigated spring wheat crops in Mexico. Many other aspects of the experiments referred to have been published (see below). This paper integrates published and unpublished data from these experiments, new data from unpublished experiments, and on occasions published literature of other workers.

MATERIALS AND METHODS

Most cited experiments were carried out in north-west Mexico at the Centro de Investigaciones Agricolas del Noroeste (CIANO, latitude 27° N, altitude 40 m) during the winter seasons 1970–1 to 1974–5 and are described in Fischer (1975), Fischer & Maurer (1976) and Fischer & Stockman (1980). Unpublished experiments at CIANO, and experiments of Wall (1979) there in 1975–6 to 1977–8, were conducted under similar conditions of management. Reference will also be made to experiments located along an altitudinal transect in central Mexico (latitude 19–20° N, altitude 60–2640 m) during the winter-spring of 1973–4 and 1974–5; these are described in Midmore, Cartwright & Fischer (1982, 1984). All experiments were managed well with irrigation, high fertility, adequate weed and disease control, and used high yielding semidwarf cultivars with little or no sensitivity to vernalization (for example Yecora 70, Sonora 64, Siete Cerros 66). Temperature was measured in standard meteorological screens and solar radiation measured with silicon photovoltaic cell sensors, which were regularly checked against an Eppley pyroheliometer. Mean climatic data of the CIANO site are shown in Table 2.

One unpublished experiment was conducted at the Ginninderra Experiment Station near Canberra, Australia (latitude 35° S, altitude 500 m), in 1981 using a crop of the semidwarf cultivar Egret, sown on 27 April under optimal management including supplemental irrigation. Portions of the crop were shaded (50% shade cloth) beginning at flag leaf emergence on 30 September and lasting until 13 October; anthesis occurred on 24 October. Mean solar radiation and temperature were 20·9 MJ/m^2/day and 12·4 °C, respectively, between 30 September and 24 October.

The number of kernels/m^2 (K) was calculated from the grain yield and mean kernel weight obtained from individual quadrat harvests at maturity; spikes were threshed and winnowed carefully in order to retain all grain. The coefficient of variation of K thus measured averaged about 8%; with 3–5 replicate blocks in each experiment, this gave standard errors of about 4% of the mean, which imposes an upper limit on the closeness of prediction of the number of kernels from crop-independent variables. Reference is also made to leaf area index (LAI); this was determined from crop sampling and included the projected area of green stems and leaf sheaths. Above-ground dry weight and spike dry weight were also determined by crop sampling.

Traditionally determination of K has been considered in terms of its constituent numerical components, i.e., numbers of plants, tillers, spikes, spikelets, florets and kernels. This analysis is of limited value because of the compensation which occurs between successive numerical components. Since this compensation probably reflects competition for limited assimilate, I intend to consider K as the result of accumulation of dry matter in growing spikes. This approach derives support from Willey & Holliday (1971), Fischer (1975), and Gallagher (1979), and from the observation by Fischer (1983) that for a given cultivar under a wide range of well-watered conditions the number of florets in a spike at anthesis was directly proportional to spike dry weight at anthesis (slope about 1 floret per 10 mg for the cultivar Yecora 70). Fischer (1983) and Fischer & Stockman (1980) propose that K be considered as the product of spike dry weight (g/m^2) at anthesis, and the number of kernels per unit of spike dry weight. Spike dry weight in turn is the resultant of, first, the duration of the period of rapid spike growth which I assume lasts from penultimate leaf appearance until anthesis (about 300 day degrees above 4·5 °C in the cultivar Yecora 70), and, secondly, the crop growth rate and dry weight allocation to spikes during this period. The number of kernels per unit of spike dry weight contains two temporally-separate components: the number of competent florets (i.e. florets judged to have fertile parts) per unit of spike dry weight at anthesis, and the number of kernels per floret, the latter depending on the distinct processes of anthesis, pollination, fertilization and subsequent kernel survival.

RESULTS AND DISCUSSION

Responses to variation in solar radiation

Number of kernels and its components, spike and chaff weight

Figure 1 illustrates a typical response in K to single 14-day shading (67% intensity of shading) periods at CIANO (Expt 74A in Fischer, 1975); it is also evident that there is no unusual variation in the amount of solar radiation above the crop which might explain sensitivity to shading just before anthesis. Shading periods which commenced after the date of 50% anthesis did not affect K; those ending before 23 days before 50% anthesis had only small and insignificant effects. Temperature averaged 14 °C during the 30-day period preceding anthesis, and LAI was 7 at its onset.

A more precise and general example of the K response to shading is provided by an unpublished 1974–5 experiment at CIANO comprising nine

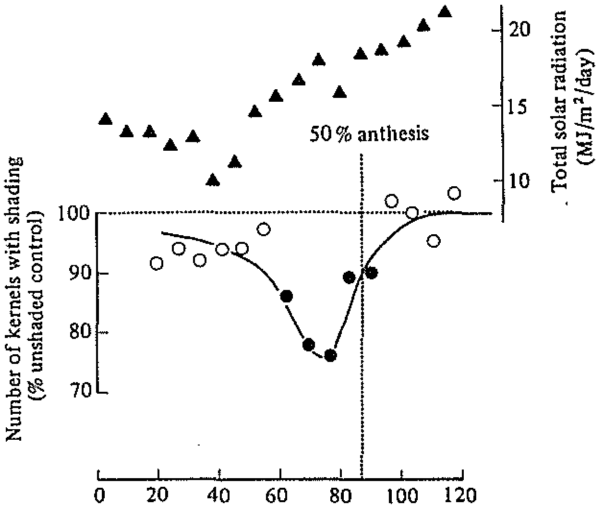

Fig. 1. The effect of single 14-day shading periods (67 % shade intensity) at various times after sowing on the number of kernels in Yecora 70 wheat at CIANO in 1973–4, Mexico (unpublished data of Expt 74A in Fischer, 1975). Each circle represents the centre of the shading period, solid symbols are significantly lower than control. Triangles show mean solar radiation during the experiment. Control number of kernels was $170 \times 10^2/m^2$.

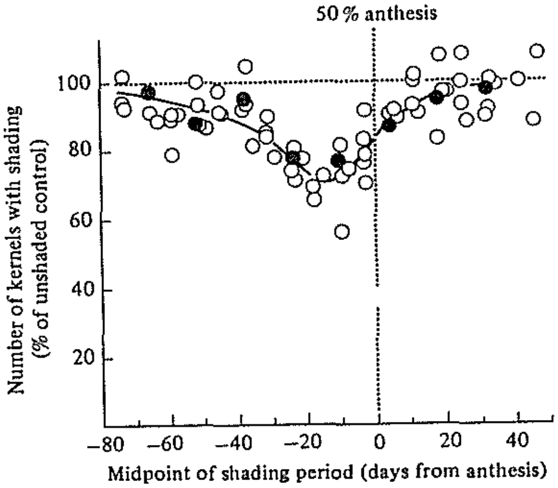

Fig. 2. The effect of single 28-day shading periods (55 % intensity) on nine semidwarf wheat cultivars at CIANO in 1974–5. Each circle represents the centre of a shading period for a particular cultivar, solid symbols refer to the cultivar Yecora 70.

semidwarf cultivars exposed to single 28-day shading periods of 55 % intensity (Fig. 2). The general relationship suggests that shading periods ending by 45 days before anthesis or starting at anthesis reduce K less than 5 % (which was estimated not to be statistically significant). Peak sensitivity occurred with shading centred about 15 days before anthesis, when K was reduced on average by 28 %. There did not appear to be a significant cultivar by shading interaction. Mean temperature and solar radiation during the month before the average date of 50 % anthesis (24 February) were 15 °C and 14·7 MJ/m²/day, respectively.

Over the five seasons 1970–1 to 1974–5, in eight experiments Yecora 70 was exposed to single short shading periods of varying intensity and timing. In order to obtain a general summary of responses to shading, the absolute change in K and its components caused by shading within (but not outside) given 30-day periods was regressed against the reduction in incident radiation with the particular shading; data were pooled across all experiments having shading in the specified period (Table 3). For any given period, radiation values ranged from control levels similar to those shown in Fig. 1 down to values about one half of control. A less precise analysis was presented in Fischer (1975) when only data from four seasons (1970–4) were used and these were uncorrected for effect of year and experiment.

Greatest response of K to radiation change (slope in Table 3) was found in the 60–90 days from sowing (i.e. the 30 days prior to anthesis; 50 % anthesis occurred on average 91 days after sowing, range 88–98 days). After this period the response was low, but before it some response was evident. In the 60–90 day period all three numerical components (number of spikes/m², number of spikelets per spike and number of kernels per spikelet) also showed significant responses to radiation change. Considering that the unshaded control received on average 16·7 MJ/m²/day during 60–90 days after sowing and had on average 167×10^2 kernels/m², 436 spikes/m², 19·4 spikelets/spike and 1·98 kernels/spikelet, the regression slopes in Table 3 for the 60–90 day period amount to relative sensitivities (percentage change in component per percentage change in radiation) of 0·58, 0·25, 0·08 and 0·32, respectively. Thus the change in the number of spikelets per spike was a relatively small part of the change K, while those in number of spikes and number of kernels per spikelet were approximately equal and substantial contributors.

Table 3 also shows the responses to radiation of chaff dry weight. Chaff dry weight determined at maturity is used because spike dry weight at anthesis was not measured. Unpublished data from other experiments indicate that dry weight of the

Table 3. *Slope and standard error for the linear relationships of the number of kernels and its components to total solar radiation in given periods; Yecora* 70, *CIANO*, *Mexico* 1970–5

Period (days from sowing)	No. of crops	Slope (±standard error)				
		No. of kernels/MJ	No. of spikes/MJ	No. of spikelets per spike/MJ ($\times 10^3$)	No. of kernels per spikelet/MJ ($\times 10^3$)	Chaff dry weight (g/MJ)
15–45	15	4·9±0·80	0·07±0·046	2·7±0·54	−0·14±0·215	0·12±0·033
30–60	17	6·3±3·38	0·04±0·087	−1·5±2·18	0·69±0·306	0·21±0·079
45–75	21	12·3±4·09	0·22±0·038	0·8±1·50	0·53±0·483	0·24±0·054
60–90	26	19·3±2·26	0·22±0·035	3·0±0·92	1·26±0·303	0·18±0·047
75–105	24	11·0±2·42	0·16±0·057	0·7±0·67	0·58±0·392	0·11±0·054
90–120	21	2·1±0·60	0·04±0·039	0·2±0·44	−0·02±0·266	0·04±0·023

spike (without grain) consistently increases from anthesis to maturity in Yecora 70 by approximately 15%. Chaff dry weight was significantly related to the amount of radiation in most periods up to anthesis. In turn change in K was closely related to change in dry weight of chaff (r values of more than 0·7 for the first four periods of Table 3, with slopes of 28, 30, 53 and 73 kernels/g respectively; because of error in estimating chaff weights slope estimates are biased downwards).

The period of shading in the Australian experiment corresponded to the 60–90 day interval in the Mexican experiments (i.e. the 30 days preceding anthesis). The responses at maturity to shading (Table 4) were similar to those seen in Mexico, with supporting data being provided by sampling at anthesis, in particular the response in spike dry weight which matches that in final number of kernels. Based on the mean solar radiation of 22·4 MJ/m²/day during the 13-day shading period, it is possible to calculate a K response to radiation reduction of 22 kernels/MJ and a chaff weight response of 0·23 g/MJ, close to the figures of 19·3 kernels/MJ and 0·18 g/MJ, derived in Mexico.

Table 4. *Response of wheat to* 13 *days of* 50% *shading during the interval* 24–11 *days before* 50% *anthesis; unpublished data, cv. Egret, Ginninderra, Australia,* 1981

Variable	Control	Shaded	S.E.
	At anthesis*		
No. of spikes/m^2	598	553	19·9
No. of florets/spike	32·3	30·6	1·29
Spike dry weight (g/m^2)	194	161	7·4
No. of florets per g spike dry wt. at anthesis	102·3	103·3	2·1
	At maturity		
No. of kernels (100/m^2)	175	143	7·5
No. of spikes/m^2	592	546	18·6
No. of kernels/spike	29·6	26·1	1·09
Chaff dry weight (g/m^2)	203	166	7·4
No. of kernels per g chaff weight	86·4	86·3	2·46
No. of kernels per g spike dry wt. at anthesis	90·2	88·8	—

* Sampled on 28 Oct.; 50% anthesis on 24 Oct. (control) and 25 Oct. (shaded).

The observed responses to radiation change in the critical period 30 days before anthesis will now be considered in terms of the hypothesis, mentioned earlier, that assimilate supply determines K. Shading in this period delayed the date of 50% anthesis only slightly (0–3 days); this effect is ignored in assuming that the duration of the period of spike growth was unchanged.

Crop growth rate

Shading reduced above-ground crop growth rate in direct proportion to the radiation reduction (Fig. 3*a*), and in direct proportion to the reduction in absorbed radiation, since all crops had reached full light interception before 60 days after sowing. The average crop growth rate of the unshaded control crops was 18·7 g/m²/day, and the average growth per unit of incident total solar radiation 1·14 ± 0·08 g/MJ. This close relationship between crop growth rate and radiation was confirmed by independent growth studies on unshaded crops in north-west Mexico (R. A. Fischer, unpublished). Above-ground crop growth rate at full light interception ranged from 11 to 26 g/m²/day and was linearly related to mean daily solar radiation (range 10·3–24·7 MJ/m²/day, $r = 0{\cdot}80$, D.F. = 65, slope = 0·77 ± 0·071 g/MJ). In contrast to Fig. 3(*a*) the relationship did not go through the origin and growth relative to radiation increased as radiation declined. Notwithstanding the different slopes (1·14 from shading, 0·77 from natural variation), it appears that crop growth rate during the 30 days

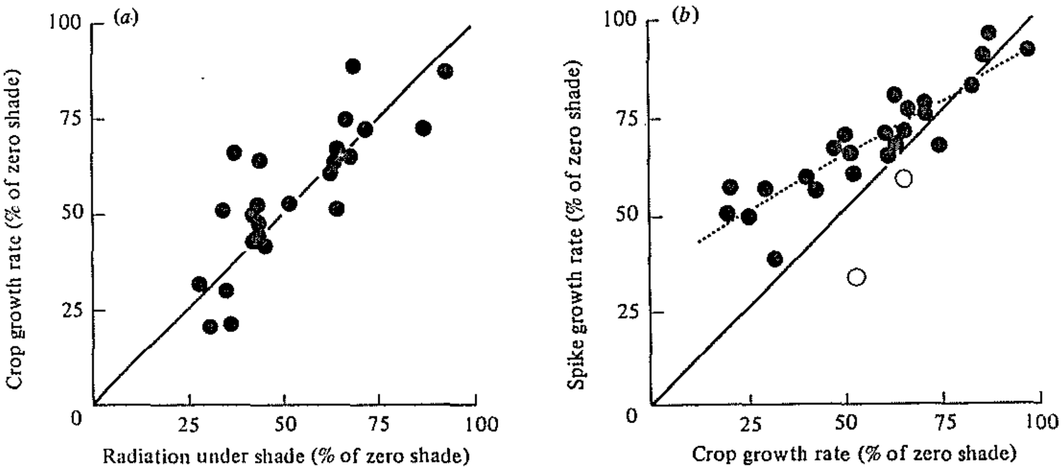

Fig. 3. The effect of shading of various shade intensities (13–70 %) and durations (20–25 days) in the approximate period 30 days preceding anthesis on (*a*) above-ground crop growth rate as a function of measured solar radiation under the shade and (*b*) spike dry weight accumulation rate as a function of crop growth rate (open symbols 1975 experiment). Yecora 70 crops at CIANO, Mexico, over period 1970–8. The solid lines represent the 1:1 relationships.

prior to anthesis is closely related to solar radiation. Gallagher & Biscoe (1978) have also pointed to the closeness of this relationship but much of the variation in their relationship was derived from LAI variation.

Partitioning of dry weight

Spike dry weight at 30 days before anthesis, as determined by various crop samplings, was negligible (< 10 g/m^2) in terms of total crop dry weight. However, the proportion of the increase in total dry weight allocated to the spike over the next 30 days (partitioning coefficient) averaged 0·44 for the unshaded crops of Yecora (with a tendency for a lower ratio in the first one-third of the interval). Figure 3(*b*) reveals that the spike partitioning coefficient increased as crop growth was reduced by shading. Willey & Holliday (1971) have pointed to a similar effect in an experiment of Puckridge & Donald (1967) when crop growth rate declined due to extremely high plant density. Probably another reflexion of this effect in our data is the fact that slope of the chaff dry weight *v.* radiation relationship (0·18 g/MJ in Table 3) is less than one would expect with unchanged partitioning (i.e. approximately 0·77 or $1{\cdot}14 \times 0{\cdot}44 = 0{\cdot}3$ or 0·5 g/MJ).

These results contrast with those of Fischer & Stockman (1980) and Stockman, Fischer & Brittain (1983) who concluded, largely from phytotron experiments, that partitioning to the spike was unaffected by shading. One reason for this difference may be the higher concentration of water soluble carbohydrates commonly found in stems of unshaded field crops (Fischer & Stockman, 1980); this pool of assimilate behaves as a low priority reserve, decreasing under shading presumably so as to buffer other sinks such as growing spikes against the reduced supply of assimilate (Wall, 1979). A second reason may be that the phytotron plants had only one culm; in the field crop the inevitable presence of higher order tillers which do not bear spikes in the control crop yet amount to 5–10 % of total anthesis dry weight would modify the overall response, since they are likely to be suppressed sooner in shaded crops. Finally it is worthwhile noting that for shading centred in the early half of the 30-day period, both in the phytotron (Fischer & Stockman, 1980) and the field (studied only in the 1975 experiment, see Fig. 3(*b*)), partitioning to the spike actually suffered under shading, suggesting that the priority of the growing spike as a sink for assimilate may increase as anthesis is approached.

Florets and kernels per unit spike dry weight

The second aspect of the proposed model of *K* determination refers to the number of florets and kernels formed per unit of dry weight investment in spikes at anthesis. In the Australian field experiment spike dry weight was measured at 4 days after anthesis (Table 4); florets and kernels per unit spike weight at anthesis were unaffected by shading. In the crops of Yecora 70 studied by Wall (1979), the number of kernels per unit spike dry weight can be calculated and appears to have been unaffected or even slightly increased by his shading treatments. In the Yecora 70 crops of Table 3, number of kernels/chaff weight, as an approximate estimate of number of kernels/spike dry weight, was calculated: it was generally unaffected by shade (overall mean 66 ± 3·0 kernels/g), with the exception of two of the crops receiving heavy shading (more than 55% shading intensity) in the 60–90 day interval (giving mean radiation receipt of less than 8·5 MJ/m^2/day); for these two exceptions the value was nearly half that of the control. Heavy shading before anthesis depressed the number of florets, and hence kernels, per unit spike or chaff weight in several phytotron experiments (Fischer & Stockman, 1980), but not in others (Stockman *et al.* 1983); however, in every case the number of kernels per competent floret appeared to be little affected by shading. This relative insensitivity of the number of grains set, by definition a post-anthesis event, to reduced radiation is confirmed in Fig. 1 and Fig. 2 and in several additional experiments in Mexico when 50–60% shading commencing at or within a few days of 50% anthesis consistently failed to affect K. Severe post-anthesis shading (more than 70%) in phytotron experiments did reduce the number of kernels per competent floret (Wardlaw, 1970; Sofield *et al.* 1977), but the relevance to field environments of such treatments is uncertain.

Responses to additional radiation

The question arises as to whether responses to additional light are the reverse of those to shading. In so far as control conditions were often cloudless in north-west Mexico this question may not be so relevant, but in a more general context it is critical. Explicit field experiments with wheat on this question are limited to preanthesis thinning studies (removal of whole rows) where extra light intercepted by remaining plants represents, albeit imperfectly, extra radiation falling on a crop canopy. Positive responses of K (and of number of spikes and of kernels per spikelet) with crop thinning in experiments in Mexico agreed, at least qualitatively, with shading responses (Fischer & Laing, 1976). Limited measurements of spike dry weight in one of these experiments supported the conclusion from the shading work that, although spikes become larger, partitioning to the spike may decrease relative to other sinks as radiation received in the 30 days prior to flowering increases; this is probably related to the many later developing tillers which survived following thinning and eventually produced spikes. Measurements of chaff dry weight in the 1973–4 experiment of Fischer & Laing (1976) suggest that preanthesis thinning did not affect the number of kernels per unit chaff weight, despite large increases in chaff weight. Increased light intensity was tested on single stemmed plants in one phytotron experiment and, while increasing spike dry weight and K it did not alter partitioning to the spike or the number of kernels per unit spike dry weight (Stockman *et al.* 1983).

Response to early shading

Another question arises from the observation that radiation reduction in periods before 30 days before anthesis had small but significant effects on K and chaff weight (Table 3). It is not clear whether this can be simply explained in terms of after-effects of shading on leaf area or photosynthetic activity and hence crop growth rate during the critical 30 days before anthesis, or whether direct effects on spike morphogenesis (significant in the case of the number of spikelets per spike in the 15–45 days period in Table 3) have an after-effect on spike growth in later stages. Under the Mexican conditions the early shading treatments, while markedly reducing LAI at the end of shading, are unlikely to have delayed the attainment of full light interception enough to reduce light interception in the critical period. However, measurements of crop growth beyond the end of shading were not made, and further work is required. In the Australian field experiment crop growth rate was depressed 20% relative to the control over the 15-day period following removal of shades.

Conclusion

A quantitative relationship between K, the number of kernels, and intensity of radiation incident on the crop, particularly in the 30 days prior to anthesis, has been demonstrated. However, it is not possible to be certain that a complete explanation of this linear relationship lies in the reduction of assimilate available for spike growth. In part the relationship is apparently explained by well documented effects of radiation on crop growth rate, but compensatory effects on assimilate partitioning to the spike, and failures in floret formation per unit of spike dry weight with particularly low radiation intensities, are presently not well quantified or understood. This latter effect suggests that a short period of especially low radiation may have proportionally greater effects on K than a similar reduction in total radiation over a longer period.

Responses to variation in temperature

This discussion is concerned with effects of variation in mean temperature in the range 5–25 °C which encompasses thermal regimes experienced by most growing wheat crops around the world. In the period from floral initiation to anthesis, this range in temperature is further reduced (Table 1). While K can be influenced by effects on the developing spike of extreme temperatures such as frost (Single & Marcellos, 1974) and hot spells (Smika & Shawcroft, 1980; Saini &

Table 5. *The influence of cooling and heating the wheat crop on number of kernels and components; Yecora* 70 *CIANO, Mexico, mean of* 1972–3 *and* 1973–4. *Published* (*first three columns*) *and unpublished* (*last two columns*) *data of Fischer & Maurer* (1976)

Treatment	Anthesis (days from sowing)	No. of kernels ($10^2/m^2$)	No. of spikes/m^2	Chaff dry wt. (g/m^2)	No. of kernels/g chaff wt.
		11–39 days after sowing			
Control	85	138	392	228	59·8
Heating	78	139	470	235	59·2
		40–67 days after sowing			
Cooling	86	152	383	233	65·2
Control	85	121	368	214	56·5
Heating	78	91	319	173	54·5
		68–92 days after sowing			
Cooling	88	136	416	248	54·3
Control	85	139	390	222	62·0
Heating	85	123	352	191	64·2
S.E.	1·2	3·0	12·4	5·1	2·59

Aspinall, 1982), no consideration is given here to these phenomena.

Field observations

Fischer & Maurer (1976) reported the effect of heating and cooling 1 m^2 portions of wheat crops enclosed in transparent chambers in experiments in Mexico. For 4-week periods mean air temperatures were 2–7 °C above, or 1–2 °C below, ambient which averaged close to 15 °C in this study. The largest negative effects of increased temperature on K occurred in the period immediately before anthesis (Table 5), when it is possible to calculate that K decreased about 4% for a 1 °C increase in mean temperature over 30 days. The role of assimilate supply to growing spikes in the temperature responses of Table 5 is suggested by the close correlation between K and chaff dry weight at maturity ($r = 0{\cdot}86$; D.F. = 6; slope = 64 kernels/g). At the same time the number of kernels per unit of chaff dry weight was not consistently affected by temperature. Effects on crop growth rate were not measured in these experiments, but variation in anthesis date (Table 5) does indicate that higher temperature accelerated development and presumably reduced the period available for spike growth.

There appear to be no other examples of experimental variation in temperature in the field. Variation in temperature without concomitant variation in radiation may be achieved by experiments located along altitudinal transects (e.g. Cackett & Wall, 1971; Midmore *et al.* 1984). The latter reference describes irrigated high fertility plantings of 13–19 semidwarf cultivars in central Mexico (latitude 19° N). Over 2 years at sites between 940 and 2640 m above sea level seven sowings received approximately similar solar radiation in the 30 days before anthesis (17·9–24·5 MJ/m^2/day and unrelated to mean temperature), and intercepted nearly all of it during this period. Across these sowings mean temperature in the period ranged from 13·9 to 22·3 °C; K which varied from 120 to 226 × $10^2/m^2$ was closely and negatively related to mean temperature (T):

$$K = 32600 - 945T \; (r = -0{\cdot}88, \text{D.F.} = 5).$$

According to this relationship, K decreased 4 and 7% per degree at 15 and 20 °C, respectively.

For these crops K was closely related to spike dry weight at anthesis ($r = 0{\cdot}86$), with the number of kernels per unit spike weight varying relatively less (73–94/g, mean 79·7 ± 2·6) and supporting the idea that temperature effects are related to assimilate accumulation in the growing spike. However, can this variation be related to the proposed determinants of spike dry weight, namely crop growth rate, assimilate partitioning or development rate? Whilst K was closely associated with total dry weight at anthesis ($r = 0{\cdot}89$, range 674–1402 g/m^2), it was not related to crop growth rate in the 30 days preceding anthesis ($r = 0{\cdot}49$, range 18–29 g/m^2/day); nor was crop growth rate related to temperature. The association of K with total growth very likely reflects a common causal factor, namely rate of development, summarized in the number of days from sowing to flowering, to which K was closely related ($r = 0{\cdot}93$, range 61–109 days). Partitioning of dry matter to the spike changed little at least in terms of the proportion of spike to total dry weight

Table 6. *Decrease in duration from spike initiation to anthesis in wheat with rise in mean temperature**

Source of data	Decrease in duration per 1 °C rise in temperature at 15 °C (%)	Estimated basal temperature† (° C)	Reference
Controlled environment	7	0·5	Friend, Fisher & Helson (1963)
Controlled environment	10	5·0	Rawson (1970)
Controlled environment	9	4·5	Rahman (1977)
Controlled environment	10	4·8	Warrington, Dunstone & Green (1977)
Controlled environment	8	2·6	Rawson & Bagga (1979)
Field Canada	10	5·9	Robertson (1968)
Field Mexico	9	4·1	Midmore *et al.* (1982)
Field World	5	5·1	Angus *et al.* (1981)
Overall mean	8·6	4·1	

* With the exception of Angus *et al.* (1981), linear model was used whereby the reciprocal of duration was plotted against mean temperature.

† Temperature at which extrapolated reciprocal of duration equals zero.

at anthesis which varied from 22 to 26% (mean 23·3 ± 0·7). These results therefore suggest that the major detrimental effect of higher temperature on K in this case operated via accelerated development.

That temperature effects on crop growth rate in the 30 days or so before anthesis were small in the above study is not surprising, because all crops were close to full light interception by a month before anthesis, and after full light interception effects of temperature on rates of photosynthesis are likely to be small, at least judging from leaf chamber studies (Austin & Jones, 1976; Takeda, 1978). Maintenance respiration losses would increase with temperature at about 10% per degree rise according to McCree (1974) for white clover. A similar relationship for a 500 g/m^2 cereal crop means this loss would increase 0·5 g/m^2/day for a 1 °C rise at 15 °C, representing a decrease of only about 2% in expected crop growth rate. No evidence for a temperature effect on crop growth rate was found in the extensive set of crop growth data collected in north-west Mexico and mentioned earlier (R. A. Fischer, unpublished).

Controlled environment responses

That accelerated development with higher temperature is the main cause of reductions in K has been suggested by many workers, who generally emphasize effects on early spike morphogenesis. It is proposed here, however, that it is the acceleration of development in the spike growth phase which is critical. Unravelling the covariance of temperature variation in successive phases of development is difficult in the field and one must look to controlled environment experiments where fortunately the effect of temperature on rate of development is unlikely to be greatly modified by artificial growing conditions. In fact when it comes to the acceleration by increased temperature of development rate between spike initiation and anthesis, controlled environment and field results lead to a similar conclusion, namely an acceleration of about 9% per degree rise in mean temperature from a mean temperature of 15 °C (Table 6). Data for intervals which correspond more closely to all or part of the spike growth period are less common, but there seems little doubt that similar relative responses occur. For example the results of Rawson & Bagga (1979) predict a reduction in the interval flag leaf emergence to anthesis of 6% or 1 day for a one degree rise in mean temperature from a mean of 15 °C. If the spike growth interval in Yecora 70 takes 300 day degrees above 4·5 °C, at 15 °C mean it is 29 days in duration, while at 20 °C it is reduced to 19 days.

Many other effects of temperature have been studied in controlled environmental experiments and while results point generally to reductions in the various numerical components of K with rise in temperature, they do not provide quantitative relationships applicable to the field. Some studies are useful in another sense. For example Rawson & Bagga (1979) showed that increased temperature in the range 12–24 °C did not affect dry weight partitioning or the number of kernels per unit unit chaff weight; the reduction in number of kernels per spike was directly proportional to the reduction in duration from double ridge to anthesis, and to that in size of the shoot and spike, a result analogous to those reported here for field studies.

Table 7. *The influence of single 14-day intervals of photoperiod extension at different times after sowing on number of kernels and its components; unpublished data, Yecora 70, CIANO, Mexico, 1974–5*

Duration of photoperiod extension* (days after sowing)	50 % anthesis	No. of kernels ($10^2/m^2$)	No. of spikes/m^2	No. of spikelets per spike	No. of kernels per spikelet
21–34	83	147	445	15·0	2·20
35–48	85	149	407	17·7	2·08
49–62	88	138	360	20·6	1·88
63–76	92	139	369	19·8	1·91
77–90	94	153	388	19·1	2·07
91–104	93	173	349	20·8	2·39
Nil = control	94	181	392	20·7	2·22
S.E.	2·1	3·8	21	0·66	0·129

* Photoperiod extended by 6 h with incandescent lamps suspended above the crop.

Conclusion

Notwithstanding the need for more information on crop growth rate and on partitioning, the results presented suggest that the consistent negative effect of increased temperature in the range 14–22 °C on number of kernels arose largely from accelerated development, and specifically a reduction in the duration of the period of major assimilate accumulation by the growing spike. The overriding importance of rate of development in the spike growth phase is supported by an unpublished photoperiod extension experiment carried out in 1974–5 season in north-west Mexico. Well managed plots of the cultivar Yecora 70 were subjected to single 14 day periods of photoperiod extension (6 h with incandescent lamps). Table 7 shows that although early photoperiod extension accelerated development more (as judged by date of anthesis) and significantly reduced number of spikelets as was to be expected, K was reduced no more than when photoperiod extension was given at the onset of the spike growth period (estimated to coincide with the 63–76 day treatment), giving development acceleration only during this latter period. Wall (1979) provides similar results for a wide range of cultivars grown in a later year.

Responses to combined variation in radiation and temperature

If the major effect of radiation on K operates via a linear relationship with crop growth rate, and that of temperature via a linear effect on rate of crop development, it is possible that K under natural conditions and full light interception can be related to the ratio of solar radiation and temperature in the critical preanthesis period. Nix (1976) defines this ratio as the photothermal quotient (Q), being mean daily total solar radiation for an interval, divided by the mean temperature less 4·5 °C, and having units MJ/m²/day/degree. The figure of 4·5 °C is close to the mean basal temperature derived from Table 6. Q can be considered as an index of growth per unit of developmental time. Some data sets for testing the utility of this index were provided by the Mexican studies.

Effect of weather variation

Well managed irrigated crops of the cultivar Yecora 70 were planted at the optimum time (late November–early December) at CIANO in each of seven seasons (1970–1 to 1977–8, excluding 1976–7 when there was no appropriate planting). The substantial variation in K between these seven crops was closely related to the small weather changes in the 30 days period prior to anthesis (Table 8, column *a*). The relationship with Q was

Table 8. *The relationship of number of kernels to mean solar radiation, mean temperature and mean photothermal quotient (see text) in the 30 days preceding anthesis**

	(*a*)	(*b*)
Size of sample	$n = 7$	$n = 15$
No. of kernels, range ($10^2/m^2$)	129–190	47–227
Correlation coefficients		
No. of kernels *v.* solar radiation	0·88	0·67
No. of kernels *v.* mean temperature	−0·75	−0·75
No. of kernels *v.* photothermal quotient	0·92	0·88
Solar radiation *v.* mean temperature	−0·51	0·25

* (*a*) refers to crops of Yecora 70 sown in late November–early December at CIANO in each year from 1970 to 1977 (except 1976). (*b*) is for the mean of eight semidwarf cultivars sown at five sites in Mexico over the period 1973–5.

Thorne & Wood (1987)

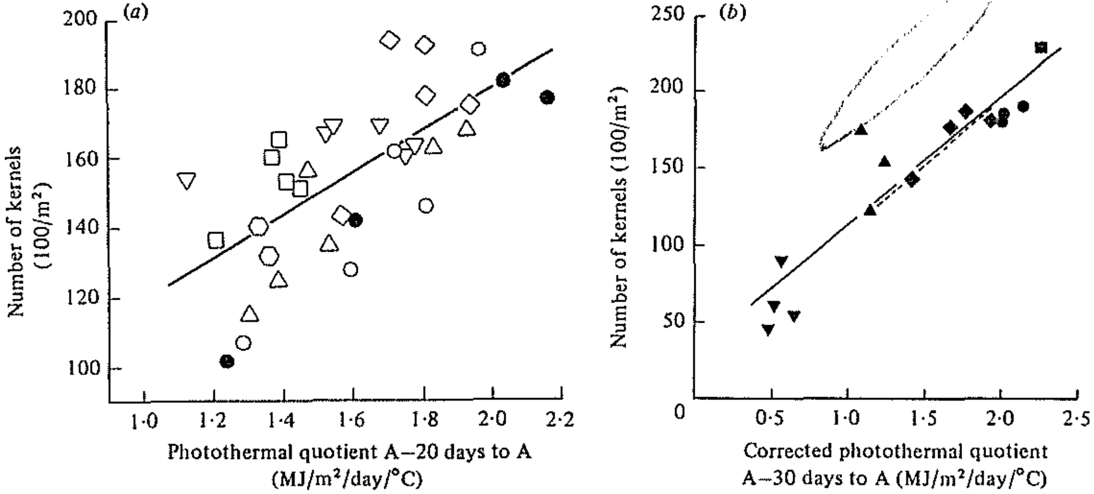

Fig. 4. The number of kernels as a function of mean photothermal quotient. (*a*) Yecora 70 crops at CIANO in 1970–1 (○), 1971–2 (□), 1972–3 (△), 1973–4 (▽), 1974–5 (◇), 1975–6 (⬡) and central Mexico 1973–5 (●) with various sowing dates and photothermal quotient calculated over 20 days before anthesis. The solid line is equation (3). (*b*) Mean of eight semidwarf cultivars at several sowing dates and sites in Mexico (Toluca ■, El Batan ●, Tlaltizapan ▲, Poza Rica ▼, and CIANO ◆) during 1973–5. In (*b*), the photothermal quotient was calculated over the 30 days preceding anthesis and corrected for incomplete light interception (see text). The solid line fits the eight semidwarf cultivar data (equation (4)), the broken line refers to the Yecora 70 relationship of equation (2).

closer than that with either radiation or temperature alone:

$$K = 2600+8510Q \quad (r = 0{\cdot}92,\ \text{D.F.} = 5). \qquad (2)$$

These results indicate that, in contrast to the conclusion of Thorne (1974) discounting the importance of small weather-based fluctuations in radiation and temperature, such fluctuations can have substantial effects on K. This appears to arise, first because of the heightened sensitivity of the crop just before anthesis and secondly because, at least in north-west Mexico, fluctuations in radiation and temperature tended to be negatively correlated thereby mutually reinforcing effects on K. Data were available from growth analysis to enable the estimation of total and spike dry weights at anthesis for the seven crops in Table 8 (column *a*): K was positively but not significantly related to the former (range 540–1093 g/m², $r = 0{\cdot}72$), and significantly related to the latter (range 153–245 g/m², $r = 0{\cdot}81$).

Effect of sowing date and weather

For each winter season of the 1970–5 period, a sowing date experiment was conducted under optimal management in north-west Mexico. These unpublished experiments provided a total of 27 crops of the cultivar Yecora 70 with sowing dates ranging from late October to late January, anthesis dates from mid-January to mid-April, and K from 107 to $195 \times 10^2/\text{m}^2$. Radiation ranged from 12 to 22 MJ/m²/day, and mean temperature from 14 to 19 °C in the month before anthesis. A correlation analysis was carried out between K of these crops and solar radiation, temperature and Q, calculated for 15-, 20- and 30-day periods up to and beyond the date of anthesis. The highest linear correlation was obtained with Q over the 20-day period preceding anthesis ($r = 0{\cdot}62$); for the 30-day period the correlation was lower ($r = 0{\cdot}49$). There were other significant correlations with K in the correlation matrix, but after removing the effect of Q in the 20 days before anthesis, the only significant correlation remaining was a weak one with mean temperature in the interval 40–20 days before anthesis ($r = 0{\cdot}40$). This latter positive correlation contrasts with the direction of responses to artificial temperature modification (Fischer & Maurer, 1976) and has no obvious explanation. Thus in this set of 27 crops, only 38% of the variation in K variation was associated with Q in the critical preanthesis period; with only about 15% of the variance due to experimental error (estimated from pooled error mean square), this result is only moderately satisfactory.

Development of the cultivar Yecora 70 is accelerated by increased daylength (Table 7), but unexplained deviations in K showed no significant relationships to daylength. However, these did vary clearly with year, being mostly positive in 1971–2 and 1973–4 (Fig. 4*a*). This suggests annual variation in management, rather than effects of weather, although the lowest point for 1970–1, a 31 January flowering crop, encountered unusual weather. Successive screen minima below zero were registered on 5–11 January, with the lowest recording being $-4{\cdot}2$ °C. There were no other below-zero temperatures in the 5-year period. Data from additional crops of Yecora 70 grown under optimal management were available, namely in the 1975–6 and 1977–8 crops of Wall (1979) at CIANO, and two crops grown in central Mexico in 1973 (unpublished) and two in 1974 (Midmore *et al.* 1984). Adding these to the 27 crops for 1970–5 at CIANO (Fig. 4*a*) modestly improved the relationship of K to Q:

$$K = 5800+6070Q \quad (r = 0{\cdot}71,\ \text{D.F.} = 31). \qquad (3)$$

In most of the 33 crops portrayed in Fig. 4*a*, total and spike dry weight at anthesis was measured. Excluding only the frosted crop and five crops for which there was no sampling at anthesis, K was highly significantly correlated with total dry weight at anthesis ($n = 27$, range 525–1093 g/m^2, $r = 0{\cdot}64$), and with spike dry weight at anthesis ($n = 27$, range 128–252 g/m^2, $r = 0{\cdot}66$). These relationships explain only about 40% of the variation in K: however, in view of the large error associated with the estimation of dry weight at anthesis in this study, a much closer relationship cannot be expected. Also for these crops, K was not significantly related to the number of kernels per unit of spike dry weight ($n = 27$, range 59–105/g, mean 78 ± 2/g, $r = 0{\cdot}16$).

A close relationship between K and Q permits prediction of the date of anthesis for maximum K. For example mean temperature and radiation figures at CIANO (Table 2) vary so that Q is greatest in March; assuming full ground cover before the spike growth period with all sowings, the date of anthesis giving most kernels would be towards the end of March. In practice rising spring temperatures so depress kernel weight and so increase irrigation demand that earlier anthesis, around early March, gives maximum yields (R. A. Fischer, unpublished).

Effect of site, sowing date and weather

The large set of diverse cultivars which was grown in 1973–4 and 1974–5 in central Mexico at four sites differing markedly in altitude provided an opportunity to test further the photothermal quotient concept (Midmore *et al.* 1984). Cultivars relatively insensitive to daylength and to vernalization showed the best overall performance across the 11 site-sowing date combinations comprising the study. A subset of eight such semidwarf cultivars (not including Yecora 70) is now chosen in order to examine K relationships further, since this subset was also represented at four previously unreported sowings in the 1974–5 season at CIANO. Including these gives a total of 15 site-sowing date combinations representing quite diverse radiation (range 11–25 MJ/m^2/day) and temperature (range 14–22 °C) environments under relatively similar daylengths. Again the closest correlation with K was obtained using Q (Table 8, column *b*).

Conditions were so hot at the lowland Poza Rica site in the Midmore *et al.* (1984) study that crops did not reach full light interception. Accordingly all values of radiation received and of Q experienced in the 30 days before anthesis both at this and other sites were corrected for radiation not intercepted by the crop, using measured LAI and an extinction coefficient of 0·44 (Gallagher & Biscoe, 1978). The relationship of K to corrected photothermal quotient (Q') was even better (Fig. 4*b*):

$$K = 2900+8370Q' \quad (r = 0{\cdot}93,\ \text{D.F.} = 13). \qquad (4)$$

This relationship is not significantly different from that determined for the cultivar Yecora 70 (Table 8, column *a*), and is strong evidence for the utility of photothermal quotient in predicting K in low latitude wheat crops. It is interesting that the highest mean number of kernels, 229×10^3/m^2, represents a very large yield potential: although a low-latitude sowing, its high altitude (2640 m) meant that abundant radiation was combined with low temperatures (Midmore *et al.* 1984). Spike dry weight at anthesis was measured in only the 11 central Mexican sowings of Fig. 4(*b*); K was closely correlated with spike weight ($r = 0{\cdot}96$) while the number of kernels per unit spike weight (90 ± 5/g) was relatively stable.

GENERAL CONCLUSION

Across a diverse set of well managed irrigated crops of the spring wheat cultivar Yecora 70, variation in number of kernels per m^2 (K) was quantitatively related to artificial independent variation in radiation and in temperature, and to the natural combined variation in radiation and temperature, in the 30-day period preceding anthesis. The relationships were simple, being linear and positive in the case of radiation, and linear and negative in the case of temperature. For combined variation, radiation intercepted by the crop divided by degrees of mean temperature above 4·5 °C provided an index, termed photothermal quotient, which was a simple yet reasonably precise linear predictor of K. The relationship appeared to hold for other semidwarf cultivars and for several low-latitude locations, but will vary between cultivars when the fractional allocation of dry

When spike dry wt at anthesis, was it corrected for grain content of A+(w). spikes - I think so - yes ✓

matter to spikes or the number of kernels per unit of spike dry weight at anthesis varies. For awned Yecora 70 this latter figure was 78 ± 2/g (crops of Fig. 4*a*) to be compared with 64–66 kernels/g chaff dry weight at maturity for crops of Tables 3 and 5; for Egret, also awned, it was 89·5/g (Table 4); and for the eight awned semidwarf cultivars of Fig. 4(*b*) the value was 90 ± 5/g. There was some environmental variation in number of kernels per unit spike dry weight, but its causes could not be identified apart from a negative influence sometimes with very low amounts of radiation.

Some authors have pointed to genetic upper limits to the numerical components of K, hence to K itself in crops (for example Krenzer & Moss, 1975); under conditions of high radiation and low temperatures K may be controlled by these genetic limits and not by photothermal quotient. However, the upper genetic limits to number of spikes per plant and of kernels per spike seem to be so far above their normal values in crops that these limits do not seem relevant to the field crop (Fischer, 1983).

The relationship of K to photothermal quotient, while derived empirically, is consistent with the hypothesis whereby spike dry weight at anthesis (g/m^2) is considered the determinant of K. It is proposed that radiation influences spike dry weight at anthesis primarily via linear effects on crop growth rate during the spike growth period immediately preceding anthesis, while temperature operates largely through its influence upon the duration of this period. The quantitative aspects of the relationship are summarized by the following statistics for the cultivar Yecora 70. The critical period is approximately 300 day degrees above 4·5 °C, so that a photothermal quotient of 1·5 MJ/m^2/day/degree amounts to 450 MJ/m^2. Since crop growth rate averaged 1·14 g/MJ, 450 MJ/m^2 corresponds to 513 g/m^2. The allocation of 44% of this to spike growth produces 225 g/m^2 of spike tissue at anthesis, which at a mean of 78 kernels/g for Yecora 70, corresponds to 176×10^2 kernels/m^2. This is somewhat higher than the value of 150×10^2/m^2 predicted by equation (2) in Fig. 4(*b*); the most likely explanation of this discrepancy is overestimation of the allocation percentage and/or the duration of spike growth.

It is also possible to compare the measured sensitivity of K to independent variation in radiation, and in temperature, to the sensitivity predicted by equation (2). With shading K changed by 19 kernels/MJ; equation (2) indicates 27 kernels MJ at 15 °C, a temperature appropriate to the shading experiments. The two cited cases of independent temperature variation suggested a 4% decrease in K as temperature rises from 15 to 16 °C; equation (2) has a slope of -7% per °C at 15 °C and 20 MJ/m^2/day, a value dominated by the choice of 4·5 °C as basal temperature. The discrepancies in both these comparisons also point to some inadequacies in the model used.

Taken overall I believe that consideration of the final dry weight of spikes as the *sine qua non* of kernels in the wheat crop will advance the understanding of the determination of number of kernels. For example temperature and radiation early in the life of the crop should influence K only indirectly, via effects on leaf area index, and hence intercepted radiation, during the critical period. To verify and extend this approach, however, more explicit data on the proposed components of K need to be collected. This will require careful crop sampling around anthesis, rather than intensive plant sampling early in the life of the crop.

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