Zahedi, M.; Jenner, Colin.
Analysis of effects in wheat of high temperature on grain filling attributes estimated from mathematical models of grain filling, *Journal of Agricultural Science*, 2003; 141 (2):203-212.

Journal of Agricultural Science (2003), **141**, 203–212. © 2003 *Cambridge University Press*
DOI: 10.1017/S0021859603003411 *Printed in the United Kingdom*

Analysis of effects in wheat of high temperature on grain filling attributes estimated from mathematical models of grain filling

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(*Revised MS received 6 May 2003*)

SUMMARY

Compared with growth at 20/15 °C (day/night), exposure of wheat (*Triticum aestivum* L.) plants to moderately high temperature (30/25 °C) significantly decreased grain weight through shortening the duration of grain filling, combined with small (or no) positive increases in the rate of grain filling. Several mathematical models of grain filling were assessed for their suitability as means of analysing these effects of temperature. The ordinary logistic model was found to be the most appropriate model and was used for the analysis of grain filling responses in four cultivars differing in their responses. Genotypic variation in response to temperature was observed for both rate and duration of grain filling, but the variation for the duration of grain filling among cultivars was small at the higher temperature. Significant correlation was found between single grain weight with the rate, but not with the duration, of grain filling at high temperature, which indicated an important role for synthetic processes involved in grain filling in the temperature sensitivity of wheat cultivars. As they are independent traits, both rate and duration are required selection criteria for the improvement of heat tolerance. Responses of one attribute estimated from the logistic model, the inflection point of the course of grain filling, may give insight into a temperature response that is distinguishable from that associated with the duration of grain filling. The inflection point appears to be worth including as a criterion in selecting for high temperature tolerance in wheat.

INTRODUCTION

High temperature during grain filling is an important factor limiting wheat yield in many wheat-growing areas (McDonald *et al.* 1983; Rawson 1986; Wardlaw *et al.* 1989*a*; Wardlaw & Wrigley 1994). Reduction in yield due to high temperature following anthesis results predominantly from decreases in kernel size (Wardlaw *et al.* 1989*b*). The optimum post anthesis temperature for maximum kernel weight in wheat is about 15 °C (Chowdhury & Wardlaw 1978), and each 1 °C rise in temperature above the optimum can cause a 3–5% reduction in single grain weight under both controlled environments (Wardlaw *et al.* 1989*a*) and field conditions (Wiegand & Cuellar 1981).

Genetic variation exists among wheat cultivars in the response of grain filling to high temperature (Rawson 1986; Wardlaw *et al.* 1989*a*, *b*; Hunt *et al.* 1991). Wardlaw *et al.* (1989*b*) examined the response of 66 wheat cultivars during grain development to exposure to high temperature (30/25 °C day/night). In their study single grain weight was reduced by about 60% in the most sensitive cultivars but by only 30% in the least sensitive cultivars compared with cooler conditions (18/13 °C day/night).

Both rate and duration of grain filling are independently influenced by high temperature (Jenner 1994). Sustained periods of moderately high temperature (up to 30 °C) reduce grain weight predominantly through shortening the duration of grain filling (Sofield *et al.* 1977). Each 1 °C increase in mean temperature can decrease the duration of grain filling by about 3 days (Wiegand & Cuellar 1981). The rate of grain filling is much less responsive than duration to temperature variation in the range of 20–30 °C. The

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magnitude of the changes in the rate of grain filling in this temperature range is dependent on genotype (Hunt *et al.* 1991) and environmental factors such as the availability of nutrients. The rate of grain growth declines at temperatures in excess of 30 °C (Tashiro & Wardlaw 1989). The decline in the rate of grain growth is mostly due to a decrease in the rate of starch accumulation; protein deposition is less temperature sensitive (Bhullar & Jenner 1985). The increase in the rate of dry matter accumulation in the range 20–30 °C is not always large enough to compensate for the reduction in grain weight due to shortened duration, resulting in a significant decrease in final grain weight (Wardlaw *et al.* 1980; Tashiro & Wardlaw 1989).

Genetic variation among wheat cultivars has also been reported for both rate and duration of grain filling (Nass & Reiser 1975; Bruckner & Frohberg 1987; Darroch & Baker 1990; Hunt *et al.* 1991). However, differences among genotypes for the duration of grain filling are small in relation to high temperature effects on final grain weight (Hunt *et al.* 1991), and final kernel weights of several wheat cultivars tested at 30/25 °C were highly correlated with the rate but not with the duration of dry matter accumulation. Differences in sensitivity among wheat cultivars to high temperature were therefore associated with their temperature responses in terms of the rate of grain filling.

Several mathematical models have been used to estimate grain filling parameters in wheat cultivars (Gebeyehou *et al.* 1982; Bruckner & Frohberg 1987; Loss *et al.* 1989; Darroch & Baker 1990). Measurement of the rate of grain filling is not a straightforward matter because the rate changes with time, and there is no non-destructive method for evaluating it. For these reasons there is not a generally accepted method for the estimation of the rate of grain filling. Bruckner & Frohberg (1987) and Gebeyehou *et al.* (1982) have calculated the average rate of grain growth as the ratio of maximum grain dry weight to duration estimated from quadratic and cubic polynomial curves. Some workers (Van Sanford 1985; Hunt *et al.* 1991) have used linear regression to estimate the rate of grain growth for the central section of the growth curve, which is assumed to be linear. However, Brunori *et al.* (1980) have pointed out that not all grain growth curves are linear, and some are sigmoid in shape. Indeed, many published grain growth curves, derived from selected grain positions to minimize variation between floret positions (e.g. Sofield *et al.* 1974; Tashiro & Wardlaw 1989, 1990) resemble a sigmoid rather than a linear growth curve. Thus Loss *et al.* (1989) and Darroch & Baker (1990) have estimated the maximum rate of grain filling from a logistic curve and found that the logistic curve could describe grain filling in the tested cultivars very well. Darroch & Baker (1990) suggested that polynomial functions could be appropriate only if grain weight decreases after reaching a maximum, which was not the case for the wheat cultivars used in their study, while in a logistic curve grain weight does not necessarily decrease when maximum dry matter is achieved. In barley, both logistic and Gompertz models fitted the grain filling data equally well (Koesmarno & Sedcole 1994).

Conceptually at least, analysis of grain filling data using models that are mathematically derived from growth theory could provide insights into the physiological mechanism(s) of high temperature effects on dry matter accumulation in wheat grain. Accordingly, the effects of high temperature on grain filling in four wheat cultivars differing in their temperature sensitivity have been analysed by several different models. Using the most suitable model, relationships have been investigated between estimated grain filling attributes and high temperature tolerance, and differences between the cultivars have been examined in some detail.

MATERIALS AND METHODS

The experiment was conducted in environment-controlled growth cabinets. Four spring wheat cultivars were selected, three for their comparative tolerance of high temperature (Wardlaw *et al.* 1989*b*; Hunt *et al.* 1991) (Trigo 1 [AUS-4073]; Kavko [AUS-25114], and Sun 27B [AUS-20007]), and one (Lyallpur [AUS-18804]) for its sensitivity (Wardlaw *et al.* 1989*b*). The plants (20 per pot) were grown in pots of recycled soil and kept in a growth cabinet set at 20/15 °C (day/night) as described by Zahedi *et al.* (2003). Only main shoots were allowed to grow and all tillers were removed as they emerged. The date of anthesis for each ear was recorded on the day when anthers emerged from the basal florets in the central (spikelets 3–7 numbering upwards from the first fully fertile spikelet at the base of the ear) section of the ear. On day 2 after anthesis, half of the pots of each cultivar were shifted to another growth cabinet, maintained at 30/25 °C (day/night) as the high temperature treatment. The rest of the plants were kept in the growth cabinet at 20/15 °C as the low temperature reference treatment. Pots were arranged, and rearranged regularly, inside the growth rooms under a randomized complete design with four replications. Samples were taken every 2 days (30/25 °C) and 4 days (20/25 °C) throughout the grain filling period. At each date, grains (10 per ear) were taken from the two basal floret positions of the five selected spikelets; they were oven-dried and grain weight was determined as described by Zahedi *et al.* (2003).

Five growth models were fitted to the grain filling data using the Genstat 5 Release 3.1 statistical program (Payne *et al.* 1993). Grain dry weight was used as the response variable and time (days after anthesis) was used as the independent variable. Three standard sigmoid curves (France & Thornley 1984) were fitted to the data:

Generalized logistic

$$W(t) = c/[1 + d\exp(-b(t-m))]^{1/d}$$

Ordinary logistic

$$W(t) = c/[1 + \exp(-b(t-m))]$$

Gompertz

$$W(t) = c\exp(-\exp(-b(t-m)))$$

where c estimates the final dry weight, b estimates the rate of growth (a slope parameter), m is the inflection point for time and d is the power-law parameter.

Koesmarno & Sedcole (1994) have used all three models to describe grain growth in barley. Loss *et al.* (1989) used the ordinary logistic model to fit grain filling data in some wheat cultivars, but in their equation a constant (a) related to the initial size of the grain is also considered, $W(t) = a + c/[1 + \exp(-b(t-m))]$.

In developing the logistic equation it is assumed that the amount of growth machinery is proportional to dry weight (W) and the growth rate is also modified by the availability of substrate. In the derivation of the Gompertz equation the assumption is that the substrate is not limiting, the quantity of growth machinery is proportional to the dry weight, but the efficiency of the catalytic growth decays with time due to enzyme degradation or senescence. The logistic growth curve has a smooth sigmoid behaviour but the Gompertz curve shows a longer linear period about the inflection point. The Gompertz equation involves three parameters but the inflection point does not occur at the halfway point in the growth curve, as occurs with logistic curves (France & Thornley 1984). Two logistic models outlined in Darroch & Baker (1995) were also included in the analysis.

The duration and maximum growth rate for each curve fitted are calculated as follows:

Model	Duration	Maximum growth rate
Generalized logistic	$m-(1/b)\ln[(1{\cdot}053^{d}-1)/d)$	$[bc/(1+d)^{1+1/d}]$
Ordinary logistic	$(bm+2{\cdot}944)/b$	$bc/4$
Gompertz	$(bm+2{\cdot}970)/b$	$bc\exp^{(-1)}$

The Gompertz model was fitted with the sense = left option.

RESULTS

Growth models and fitting grain filling data points

The data were fitted to five growth models in order to select one that best fitted them. As they are analogous, values estimated for the three-parameter model of Darroch & Baker (1995) and the ordinary logistic model of France & Thornley (1984) were identical. The simpler two-parameter model of Darroch & Baker (1995) did not fit the data as well as the other four models, possibly because either an inappropriate value was assumed for W_o, or because days after anthesis were used instead of growing degree days. No estimates calculated for either of the Darroch & Baker (1995) models are reported here.

Values of the adjusted R^2 and the residual mean squares (residual MS) derived from the other three growth models were used as the basis for comparison (Table 1). There were only small differences in adjusted R^2 between the models and the data fitted all three models with R^2 values higher than 99 %. Comparisons between predicted and actual dry matter accumulation in cultivars Lyallpur and Sun 27B at both temperatures for the best fitting model, the ordinary logistic, are illustrated in Fig. 1. The curvilinear shape of the growth curve was clearly evident for all four cultivars (only two are displayed in Fig. 1). The data did not fit a straight line as well (R^2 below 99 %) as the ordinary logistic model. Linear regression analysis (see later in Table 6) was however conducted to estimate the 'sustained rate' of grain filling and even when the analyses were confined to the middle 7–9 points in the curves, the R^2 values were lower than those derived from the ordinary logistic calculations.

Growth models and grain-filling estimation

A comparison between the three models in estimating the rate of grain filling, the duration of grain filling and final grain weight in all four cultivars grown at 20/15 °C and 30/25 °C is presented in Table 2. The models gave values that differed little from each other for the rate of grain filling, especially at high temperature. Differences between the models in estimating the duration of grain filling were greater than observed for the estimates of the rate of grain filling. Under both temperatures and in all varieties there was a consistent tendency for the Gompertz model to overestimate the duration of grain filling compared with the other models by a large margin. There were also small differences between the growth models in their estimation of final grain weight, with estimates for the Gompertz model being greater than for the

Table 1. *Comparative statistics for three growth models fitted to the grain filling data of four wheat cultivars grown at 20/15 °C and 30/25 °C (day/night temperature)*

		Adjusted R^2		Residual mean squares	
		Day/night temperature (°C)			
Cultivar/Model	Number of parameters	20/15	30/25	20/15	30/25
Lyallpur					
Generalized logistic	4	99·5	99·4	1·575	0·569
Ordinary logistic	3	99·5	99·4	1·491	0·518
Gompertz	3	99·2	99·2	2·543	0·692
Sun 27B					
Generalized logistic	4	99·9	99·8	0·288	0·153
Ordinary logistic	3	99·7	99·8	0·572	0·141
Gompertz	3	99·9	99·5	0·265	0·291
Kavko					
Generalized logistic	4	99·8	99·5	0·339	0·440
Ordinary logistic	3	99·7	99·5	0·527	0·410
Gompertz	3	99·0	99·4	1·861	0·488
Trigo 1					
Generalized logistic	4	99·5	99·5	1·289	0·604
Ordinary logistic	3	99·5	99·5	1·291	0·551
Gompertz	3	99·5	99·3	1·398	0·869

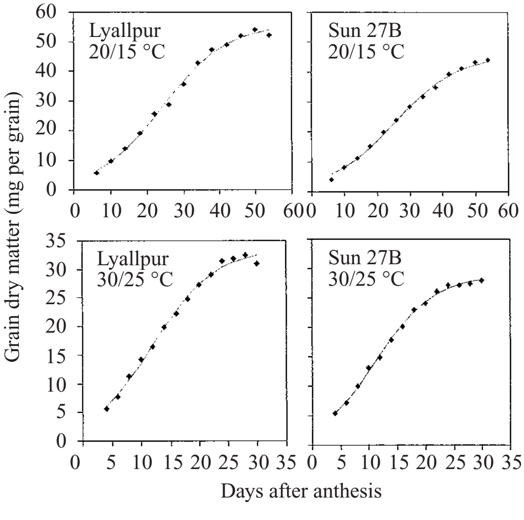

Fig. 1. Comparisons between the grain filling data and the growth curves fitted to the ordinary logistic model for two wheat cultivars, Lyallpur and Sun 27B, grown at 20/15 °C and at 30/25 °C (day/night temperatures).

logistic models. From these comparisons the logistic models appeared to be the most appropriate, and as it was the simplest, the ordinary logistic model was used for estimating grain-filling parameters reported here.

Effects of high temperature on grain-filling attributes

The results of the analysis of variance on the estimated values of grain filling attributes estimated by the ordinary logistic model are shown in Table 3. Temperature affected the four estimated attributes significantly, and there were significant interactions with cultivar for three of them.

The interaction between cultivar and temperature for final grain weight (Table 4) was highly significant. Individual kernel weight was significantly reduced in all cultivars at 30/25 °C compared with 20/15 °C, and Kavko was more tolerant of high temperature than the other cultivars with a 21 % reduction in its grain weight. Lyallpur was the most sensitive with a 40 % reduction (Table 5). Reduced grain weight in Lyallpur at high temperature was due to significantly shortened duration of grain filling with no compensating increase in the rate of grain filling. In the other three cultivars there was an increase in the rate of grain filling but it did not compensate fully for the reduced grain filling period. Although there was a significant increase in the rate of grain filling of Sun 27B at high temperature, the large reduction (28 days) in the duration of grain filling of this cultivar at high temperature caused a considerable decline in final grain weight (38 %). This made Sun 27B rank second after Lyallpur in terms of sensitivity to high temperature. Grain weight at maturity was positively but not significantly correlated at 20/15 °C with both rate ($r=0{\cdot}41$) and duration of grain filling ($r=0{\cdot}33$).

Table 2. *A comparison between the growth models in estimating grain filling parameters of four wheat cultivars grown at 20/15 °C and 30/25 °C (day/night temperature)*

	Rate of grain filling (mg/day)		Duration of grain filling (days)		Final grain dry weight (mg)	
Cultivar/Model	20/15	30/25	20/15	30/25	20/15	30/25
Lyallpur						
Generalized logistic	1·58	1·58	49·0	27·8	55·4	33·7
Ordinary logistic	1·57	1·58	50·6	27·6	56·0	33·5
Gompertz	1·49	1·58	63·9	34·2	60·9	36·0
Sun 27B						
Generalized logistic	1·13	1·42	64·7	25·7	49·0	28·6
Ordinary logistic	1·17	1·42	54·1	26·4	45·8	29·0
Gompertz	1·12	1·43	70·5	31·7	50·9	30·4
Kavko						
Generalized logistic	1·46	1·63	40·5	27·4	40·1	33·1
Ordinary logistic	1·40	1·67	44·4	26·0	41·2	32·6
Gompertz	1·33	1·65	54·1	31·9	43·6	34·6
Trigo 1						
Generalized logistic	1·66	1·91	50·4	26·1	52·9	36·1
Ordinary logistic	1·73	1·91	45·7	26·5	51·0	36·4
Gompertz	1·60	1·86	59·6	32·5	57·1	38·8

Table 3. *Probability values obtained from the analysis of variance table for grain growth parameters of Lyallpur, Kavko, Sun 27B and Trigo 1 grown at 20/15 °C and 30/25 °C, and as estimated by the ordinary logistic model*

Source	Final grain dry weight	Maximum rate of grain filling	Duration of grain filling	Time to the inflection point
Temperature	0·0001	0·0043	0·0001	0·0001
Cultivar	0·0001	0·0001	0·0035	0·0642
Temperature × cultivar	0·0001	0·4610	0·0174	0·0411

At 30/25 °C, the correlation between the rate of grain filling and final grain weight ($r = 0{\cdot}67$, $P \leqslant 0{\cdot}01$, $n = 16$) was much larger than the correlation between grain filling duration and final grain weight ($r = 0{\cdot}25$, n.s.). Final grain weight was also positively correlated with the number of days from anthesis to the inflection point but the correlation coefficient was much greater at 30/25 °C ($r = 0{\cdot}69$, $P \leqslant 0{\cdot}01$) than at 20/15 °C ($r = 0{\cdot}35$, n.s.).

The main effects of temperature and cultivar on the maximum rate of grain filling were highly significant but the interaction was not (Table 3). The maximum rate of grain filling in all cultivars, with the exception of Lyallpur, was increased at 30/25 °C compared with 20/15 °C (Table 4). Lyallpur maintained the same rate at both temperatures with a temperature quotient (Q_{10}) close to 1 (Table 5). At each temperature separately, and averaged over both temperatures, Trigo 1 had the highest value and Sun 27B the lowest for the maximum rate of grain filling.

The sustained rate of grain filling, as defined here, was estimated by linear regression and represents the rate sustained for a period during which between 80 and 90% of the final grain dry matter was accumulated. The sustained rate was calculated by sequential omission of data points from both ends of grain growth curves. As expected, estimates of this attribute (not given in detail) increased in magnitude, and there was also tendency for values of R^2 to increase, as the number of points was reduced tending at the extremes towards the values of the maximum rates appearing in Table 4. For example, at 20/15 °C the estimate by linear regression of the sustained rate for Lyallpur derived from the four points in the middle of the curve was 1·47 mg/grain per day; corresponding values for Sun 27B (five points), Kavco (five) and Trigo (five) were 0·95, 1·35 and 1·51 mg/grain per day respectively. In general the estimates of the average rates sustained during the accumulation of between 80% and 90% of the grains' total dry matter appeared

Table 4. *Grain growth characteristics of four wheat cultivars grown at 20/15 °C and 30/25 °C, as estimated by the ordinary logistic model. LSD, least significant difference; n.s., not significant*

Cultivar	Temperature (°C)	Final grain dry weight (mg)	Maximum rate of grain filling (mg/day)	Duration of grain filling (days)	Time to the inflection point (days)
Lyallpur	20/15	56·0	1·57	50·6	24·2
	30/25	33·5	1·60	28·1	12·3
Sun 27B	20/15	46·4	1·16	55·2	25·8
	30/25	29·0	1·42	26·8	11·5
Kavko	20/15	41·2	1·40	44·4	22·7
	30/25	32·6	1·67	26·0	11·5
Trigo 1	20/15	51·0	1·73	45·7	24·0
	30/25	36·4	1·91	26·5	12·4
LSD $P \leqslant 0{\cdot}05$	Cv × temp	3·1	0·24 n.s.	4·6	1·6

Table 5. *Effects of growth at 30/25 °C compared with 20/15 °C on grain growth parameters of four wheat cultivars calculated from Table 4*

Cultivar	Reduction in grain weight (%)	Q_{10} for the maximum rate of grain filling (30/20 °C)	Reduction in the duration of grain filling (%)	Reduction in time to the inflection point (%)
Lyallpur	40	1·02	45	49
Sun 27B	38	1·22	51	55
Kavko	21	1·19	41	49
Trigo 1	29	1·10	42	48

Table 6. *A comparison between the maximum and the sustained rates of grain filling in four wheat cultivars grown at 20/15 °C and 30/25 °C, estimated respectively by the ordinary logistic model and by linear regression*

Cultivar	Temperature (°C)	Maximum rate of grain filling (mg/day)	Sustained rate of grain filling (mg/day ± S.E.)	Q_{10} for the maximum rate (30/20 °C)	Q_{10} for the sustained rate (30/20 °C)
Lyallpur	20/15	1·57	1·24 ± 0·05	1·01	0·97
	30/25	1·58	1·20 ± 0·05		
Sun 27B	20/15	1·17	0·92 ± 0·03	1·21	1·15
	30/25	1·42	1·06 ± 0·06		
Kavko	20/15	1·40	1·08 ± 0·06	1·19	1·14
	30/25	1·67	1·23 ± 0·06		
Trigo 1	20/15	1·73	1·37 ± 0·05	1·10	1·05
	30/25	1·91	1·44 ± 0·07		

only a little less precise than estimates derived from shorter periods. A comparison between the maximum and sustained rates of grain filling (Table 6) shows that the cultivars maintained the same ranking for the sustained rate as they did for the maximum rate of grain filling. Ranking for the increases in the rate of grain filling at 30/25 °C compared with 20/15 °C (Q_{10}) was also identical for the maximum and sustained rates of grain filling. The values of Q_{10} in all cultivars for the sustained rate were proportionally about 4–5% smaller than for the maximum rate of grain filling. Although these smaller values of Q_{10} may indicate that the overall process of grain filling was slightly less responsive to the upward shift in temperature than was the maximum rate, the data do not indicate any genetic variation in this respect.

Duration of grain filling

The duration of grain filling was significantly reduced in all cultivars in the plants grown at 30/25 °C in comparison with those grown at 20/15 °C (Table 4) and there was a significant interaction between cultivar and temperature. Compared with the other three cultivars, Sun 27B had the longest period of grain filling at 20/15 °C. The reductions in the duration of grain filling at high temperature varied from 18 days (41 %) in Kavko to 28 days (51 %) in Sun 27B (Table 5). Significant genotypic variation existed at 20/15 °C (about 10 days difference between the longest and the shortest grain filling duration), but the variation was small at 30/25 °C and no significant differences (less than 2 days) were observed between cultivars at this temperature.

Time to the inflection point

The time from anthesis to the maximum rate (the inflection point) of grain filling (Table 4) was significantly reduced at 30/25 °C compared with 20/15 °C in all cultivars. In Sun 27B the reduction (55 %) was larger than the other cultivars (48 % in Trigo 1 and 49 % in Lyallpur and Kavko; Table 5). The time to the inflection point at 20/15 °C ranged from 23 days (in Kavko) to 26 days (in Sun 27B) but at 30/25 °C all cultivars reached the inflection point on about day 12 after anthesis.

DISCUSSION

Besides goodness of fit, physiological credibility is another criterion for judging the applicability of a model of grain filling. Preference here for a curvilinear model over a linear one was not based simply on the shape of the grain-filling curve. Although it is true (Morris 1999) that averaging individual linear growth curves, which vary in slope and in the timing of the beginning and end of the growth process ('broken-sticks'), would result in a sigmoid curve, this does not rule out a curvilinear growth model *ipso facto*. In fact, the weight of published evidence supports the view that grain growth curves are not exclusively linear or curvilinear (Brunori *et al.* 1980). The care taken in this present and other work (e.g. Sofield *et al.* 1974; Tashiro & Wardlaw 1989; Wardlaw & Moncur 1995) to select floret positions in which the grains develop synchronously reduces the likelihood of artefacts, and where this has been done many of the growth curves are clearly sigmoid. It is also germane that accumulation is not terminated simultaneously in all components of grain dry matter (Brunori *et al.* 1980) and that the rate and duration of starch and protein deposition in the grain are independent events controlled by separate mechanisms (Jenner *et al.* 1991).

As starch is the major component of grain dry matter, the kinetics of starch accumulation dominate the time-course of the final stages of grain filling. Termination of starch synthesis is due to a decline in the activity of the starch biosynthetic system in wheat (Jenner 1986 and references cited therein) and in barley (Wallwork *et al.* 1998). This decline is a gradual process, and is probably under developmental control. While grain water relations may influence grain development, there is no evidence that a sudden shift in grain water relations terminates grain filling. Tashiro & Wardlaw (1990) demonstrated that the onset of water loss from the grain, and the cessation of grain filling could occur asynchronously.

In summary the 'broken stick' model is not applicable to the work described here, but it may appear to be applicable in cases where a linear model fits the growth curve better than a curvilinear one, for example where grain filling is terminated by a very rapid loss of activity of the biosynthetic processes.

The logistic growth models tested here generally fitted the grain growth curves very well. In some cases the deviations of the predicted grain dry matter from the observed values (residual mean squares) were larger for the Gompertz model than for the logistic models. In other studies also logistic models have provided a good fit to grain filling data in wheat (Loss *et al.* 1989; Darroch & Baker 1990) and in barley (Koesmarno & Sedcole 1994). In the present study the differences between the logistic and the Gompertz models in estimating the final grain weight were small, but considerable differences appeared between the two models when they were used to estimate the duration of grain filling (Table 2). From a consideration of all of these results the logistic models described grain filling better than the Gompertz model. As the generalised logistic model involves one more parameter (d which has no self-evident physiological meaning) than the ordinary logistic model, the simpler ordinary logistic was chosen as the most appropriate model to estimate grain-filling parameters in the cultivars examined here.

It is reasonable to infer that the shape of the growth curve itself might reflect something of the nature of the processes involved in grain filling. For example, the maximum (instantaneous) rate is derived from an estimate at or close to the mid point (at the inflection point) of grain filling. From the physiological point of view, this attribute might be an indication of an upper limit to the rate of grain filling under the conditions of the experiment. Such a limit might reflect the maximum capacity of the activity of synthetic systems and/or an upper limit to the influx of nutrients into the grain.

The inflection point of the curve occurs at the instant when the rate of accumulation ceases to accelerate and begins to slow down. This point is thus a sign of a shift in developmental processes from those involved in the synthesis of dry matter towards those involved in senescence and/or decaying activity of the synthetic processes, or a slowdown in the import of assimilates into the grain.

Genetic variation among wheat cultivars has been reported for the responsiveness of grain filling to high temperature (Rawson 1986; Wardlaw *et al.* 1989*a*, *b*; Hunt *et al.* 1991). Here also there was a significant decrease in kernel weight in response to an increase in temperature from 20/15 °C to 30/25 °C, which ranged from 21 % (in Kavko) to 40 % in Lyallpur (Table 5). Lyallpur (Wardlaw *et al.* 1989*b*) and Kavko (Hunt *et al.* 1991) have previously been identified respectively as sensitive and tolerant cultivars to high temperature. Wardlaw *et al.* (1989*b*) recorded a 22 % reduction in the grain weight of Trigo 1 compared with 51 % in Lyallpur with an increase in temperature from 18/13 °C to 30/25 °C. Significant genotypic variation was observed for the duration of grain filling, but the variation between cultivars was small especially at high temperature (Table 4). Little variation among cultivars for duration of grain filling in relation to temperature effects has also been reported in other studies (Hunt *et al.* 1991; Wardlaw & Moncur 1995).

The rate of grain filling was increased in three of the four cultivars at high temperature but the reduction in grain weight due to the shortened duration was not compensated for completely by the increased rate of grain filling, as has been reported by others (Sofield *et al.* 1977; Wardlaw *et al.* 1980; Tashiro & Wardlaw 1989). However, the significant positive correlation between final grain weight with the rate ($r = 0{\cdot}67$), but not with duration of grain filling ($r = 0{\cdot}25$, n.s.) at high temperature, showed that the response of the rate of grain filling to temperature was the more important in determining the temperature sensitivity of the cultivars. This supports the results from the work of Wardlaw & Moncur (1995) who reported that the most tolerant cultivars to high temperature during grain filling were those in which the rate of grain filling was increased most by high temperature. These authors also reported that at high temperature the association between kernel weight at maturity with the rate of kernel filling was much stronger ($r = 0{\cdot}94$) than with the duration of kernel filling ($r = 0{\cdot}51$). Similar results were obtained in the field in the areas experiencing high temperature during grain filling (Bruckner & Frohberg 1987). The responses of Sun 27B illustrate however why neither rate nor duration alone can explain all variation in heat sensitivity between cultivars (Table 5). The rate of grain filling was increased as much in Sun 27B as in Kavco, but its duration was shortened so much that Sun 27B was classed as one of the most heat-sensitive cultivars. Clearly, heat tolerance is dependent on temperature responses of the synthetic system operating in the grain as well as on effects of temperature on the rate of grain development (i.e. tolerance is controlled by multiple genes; see Yang *et al.* 2002). Thus, a combination of the genetic basis for high Q_{10} in Sun 27B with cultivars less sensitive to reduction in duration could produce lines with improved tolerance to high temperature. Simultaneous selection for high grain filling rate and high grain weight would therefore seem to be feasible without the necessity to extend the grain filling period. The advantage of this strategy for developing cultivars tolerant of warm dry environments, where conditions for grain filling progressively deteriorate as the season advances, is self-evident.

The maximum rate of grain filling may be a quantitative expression of the maximum capacity of the synthetic system combined with the delivery of substrates for grain filling, but it is not sustained for long enough to be a meaningful measure of the rate of grain growth during the major phase of grain filling. Calculation of the average rate is a more pertinent estimate of the overall performance of the grain filling processes. Linear regression analysis of data taken during an arbitrarily specified portion of the grain's development was chosen as a measure of this attribute and was termed the sustained rate of grain filling (Table 6). Although the physiological significance of this attribute is not self-evident, it may reflect the robustness of the functioning of the synthetic processes and/or the delivery of nutrients to the grains.

Whether or not the two estimates (instantaneous and sustained) of the rate of grain filling are indicative of different aspects of the grain filling process, two things are clear from Table 6: (i) judging from the Q_{10} values, there are similar temperature responses for both attributes, and (ii) that by either estimation, Kavko and Sun 27B show a greater positive temperature response than does Lyallpur, with Trigo 1 intermediate between the two extremes.

The temperature quotient (Q_{10}) is a measure of the response to an increase in temperature of 10 °C. Most values of Q_{10} observed within the normal temperature range for physiological processes in temperate crops normally fall within the range 1·3–1·6. Values of Q_{10} for the rate of grain filling reported in Table 6 are below the lower end of this range and that for Lyallpur is close to or below 1·0. Such low temperature optima for grain filling are attributable to the temperature sensitivity of starch accumulation (Bhullar & Jenner 1985, 1986), and have been associated with the thermal characteristics of enzymes involved in the synthesis of starch (Jenner *et al.* 1995). Although thermal inactivation of soluble starch synthase (SSS) does not appear to be the cause of the low temperature optimum for starch synthesis in this (20–30 °C) temperature range, other thermal characteristics of SSS (K_M and efficiency) appear more likely to be the cause of temperature sensitivity in wheat (Jenner & Sharma 1997). The extent to which these latter characteristics can explain differences in temperature tolerance between cultivars is explored elsewhere (Zahedi *et al.* 2003).

Not only was the duration of grain filling shortened in Sun 27B at high temperature more than in the other three cultivars, but so also was the time to the inflection point (Table 5). The response that curtailed grain filling at high temperature in Sun 27B was evidently perceived during the first 12 days of development, long before grain filling ceased at 30/25 °C (Table 4). Such a response seems more likely an indication of an inherent developmental response to temperature in the grain rather than the impact of a harmful effect of high temperature only during the last stages of grain filling. In other words, information on both the inflection point and the duration of grain filling may distinguish between two different temperature response mechanisms. Perhaps (*inter alia*) under high temperature conditions, the length of the period to the inflection point is predictive of the amount of dry matter to be accumulated in the grains, and so may be a useful additional physiological criterion in selecting for grain filling performance at high temperature.

The modelling approach shows promise as a means of examining the effects of temperature on grain filling in wheat. The logistic model has been used in an analysis of the effects of high temperature on the metabolites and enzymes of starch synthesis in wheat (Zahedi *et al.* 2003), and also in an investigation of the effects of nitrogen supply on temperature responses of starch and protein deposition in the developing wheat grain (Zahedi & Jenner, unpublished data). Temperature responses of attributes estimated from the model appear to throw some light on physiological responses to temperature, indicating that these attributes may be useful in selecting for high temperature tolerance in wheat.

Financial assistance provided for this project by the Ministry of Science, Research and Technology of the Islamic Republic of Iran is appreciated. The authors thank Professor R. J. Baker (Saskatoon) for his helpful comments on the preparation of the manuscript for publication.

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