DYNAMICS OF EAR AND STEM GROWTH AND THE CONTROL OF GRAIN NUMBER PER EAR IN WHEAT

E.J.M. Kirby

Department of Agronomy
Institute of Agriculture
University of Western Australia

ABSTRACT

The growth of the ear and stem of the main shoot of wheat was studied from the terminal spikelet stage until anthesis. Floret number in a mid-ear spikelet increased to a maximum of ten at the time of flag leaf emergence. Floret death occurred during the period from ear emergence until anthesis. This coincided with rapid growth in length of the peduncle and with the time of maximum growth in dry mass of the ear and stem.

These results are consistent with the hypothesis that floret death is due to shortage of resources for growth. Further improvement in floret survival and number of grains per ear may come from selection for greater partitioning of dry matter to the ear and for reduced peduncle length, relative to total stem length.

KEYWORDS

Floret death, internode and ear growth, peduncle growth.

INTRODUCTION

Increases in the yield of wheat have largely been the result of an increase in the number of grains per unit area. Part of this increase has been due to an increase in the number of grains per ear, particularly in the case of improved genotypes (Gale and Youssefian, 1984).

The determination of the number of grains per ear is the integration of all the processes of development of the ear, involving several distinct phases. In sequence, these comprise the phase of spikelet initiation — determining the number of spikelets per ear; floret formation within each spikelet; a phase when some of the floret primordia die — determining the number of competent florets; and finally, pollination and fertilisation which determines the proportion of competent florets which set grains. Initiation of florets in the middle spikelets of an ear starts before the terminal spikelet is formed, and a maximum of about ten florets per spikelet is initiated (Kirby, 1974). Death of florets is first detected in the meristematic dome and in the most distal florets of the spikelet. It proceeds acropetally so that generally only from three to six florets form well

developed green anthers and carpels with large feathery, turgid stigmas, apparently with the potential for fertilisation and grain filling. Floret initiation and death occur during the phase from terminal spikelet formation to anthesis. Several studies have shown this phase is of particular importance in determining the number of grains per ear (Fischer, 1985). Stress in the pre-anthesis period reduces the number of grains per ear. This evidence and evidence from growth studies (Brooking and Kirby, 1981) has suggested that during this phase there may be insufficient resources to support the full potential for growth, resulting in competition between the ear and the stem, which may cause floret death.

There are a few detailed studies on the timing of floret death, or on internode and ear growth between terminal spikelet and anthesis. In this paper, relationships between leaf, stem and ear growth and floret development and death are described. The results are examined in relation to an hypothesis of competition for limited resources; the relation between the pattern of growth and selection for high numbers of grains per ear is considered.

MATERIALS AND METHODS

An experiment was conducted using the spring wheat cultivar Wembley. Plants were grown in 90 mm diameter pots filled with John Innes no.1 compost, in an unheated glasshouse at the Plant Breeding Institute, Cambridge. Seed was sown on 25 February and measurements were started when the terminal spikelet stage was observed. Frequent samplings were made (three to four per week), and on each sample plant the main shoot was identified for subsequent measurement. Counts were made of the number of emerged leaves, the total number of leaves, and the number of living floret primordia in a mid-spikelet of the ear (spikelet 10). On the same shoot, lengths of the elongating internodes and the length of the ear were measured. After drying for 48 h at 80 °C, the dry mass of each internode and the ear were found.

Starting at the terminal spikelet stage the ambient temperature (1 m above the bench level) was measured with an aspirated thermocouple and recorded every 30 min using a 'Solatron' datalogger. The temperature record was processed to give daily values of thermal time.
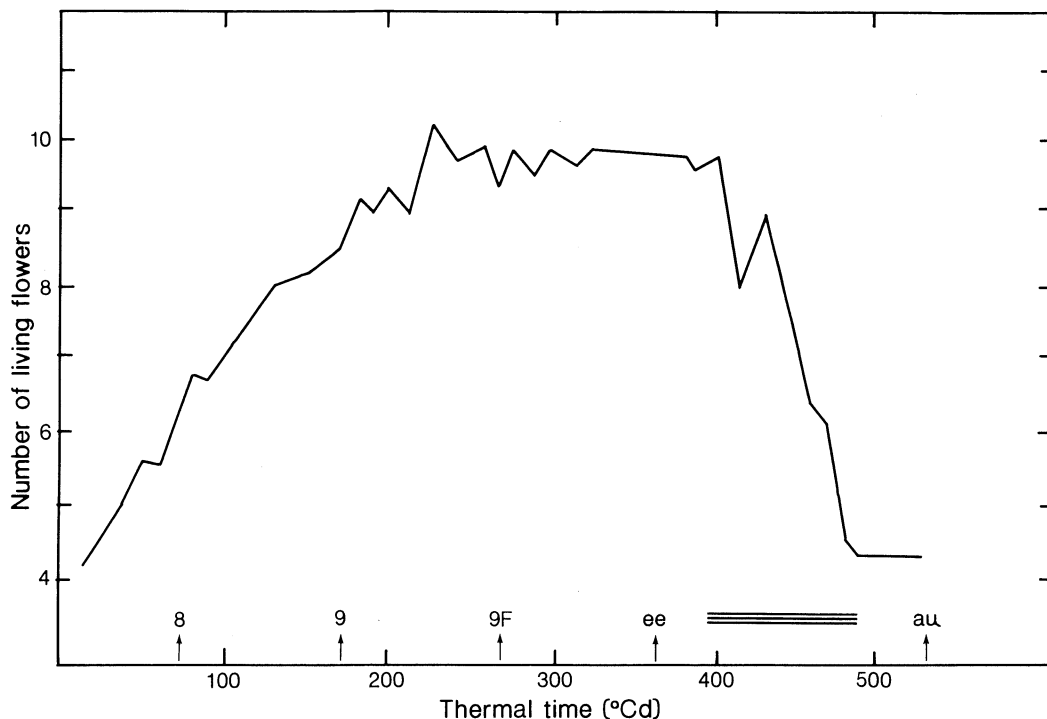
Figure 1. Number of living primordia versus thermal time. The vertical arrows mark the times of various events in the life cycle. These were 8,9, emergence of the tip of leaves 8 and 9; 9F, full emergence of leaf 9 (the flag leaf); ee, ear emergence; an, anthesis. The horizontal bar (≡) marks the period of floret death.

$$Tt = \sum_{t=1}^{t=24} (T-Tb)/24$$

where Tt is the thermal time (accumulated temperature), T is the ambient temperature, and Tb is the base temperature (0 °C). The temperature did not fall below 0 °C during the course of the observations.

Instantaneous maximum growth rates where estimated by fitting a modified logistic function (France and Thornley, 1984) to the data of length and dry mass versus thermal time.

$$Y = A + C (1 + T*exp(-B/X-M)) **1/T$$

where A, C, T, B and M are constants and X is the thermal time. The parameters were fitted using the MLP programme (Rothamsted Experimental Station).

RESULTS

The rate of leaf emergence was established from the regression of the number of leaves versus thermal time. the phyllocron (1/rate of emergence) was 101 °Cd per leaf. At terminal spikelet four floret primordia had initiated. Initiation continued until the flag leaf was emerging (220 °Cd) when about 10 florets were present (Fig. 1). No further florets were initiated. Growth and development of the florets continued, particularly of the lower florets, but no other change was apparent until the tip of the ear emerged from the leaf sheath (390 °Cd). At this time, a loss of turgor was seen, first in the meristematic dome and then in the distal florets, followed by obvious senescence of the tissue. The number of living florets declined until after about 90 °Cd from the beginning of floret death. There were four surviving florets (Fig. 1). The number of grains in this spikelet at maturity was 3.9.

Stem elongation started at internode five. The final length of this internode was rather variable but it seldom exceeded 15 mm in length. Internode six, which was the first internode to elongate, regularly started growth at about 50 °Cd (Fig. 2). As each internode grew to about half it final length, the next most distal internode commenced growth. The growth of the peduncle commenced just before the onset of floret death and it grew rapidly throughout the phase of floret death.

The pattern of dry mass growth was similar to that for length growth. The rapid rate of dry matter accumulation started when an internode was about one third of its final length and dry matter accumulation continued for some time after maximum length was attained. While the dry
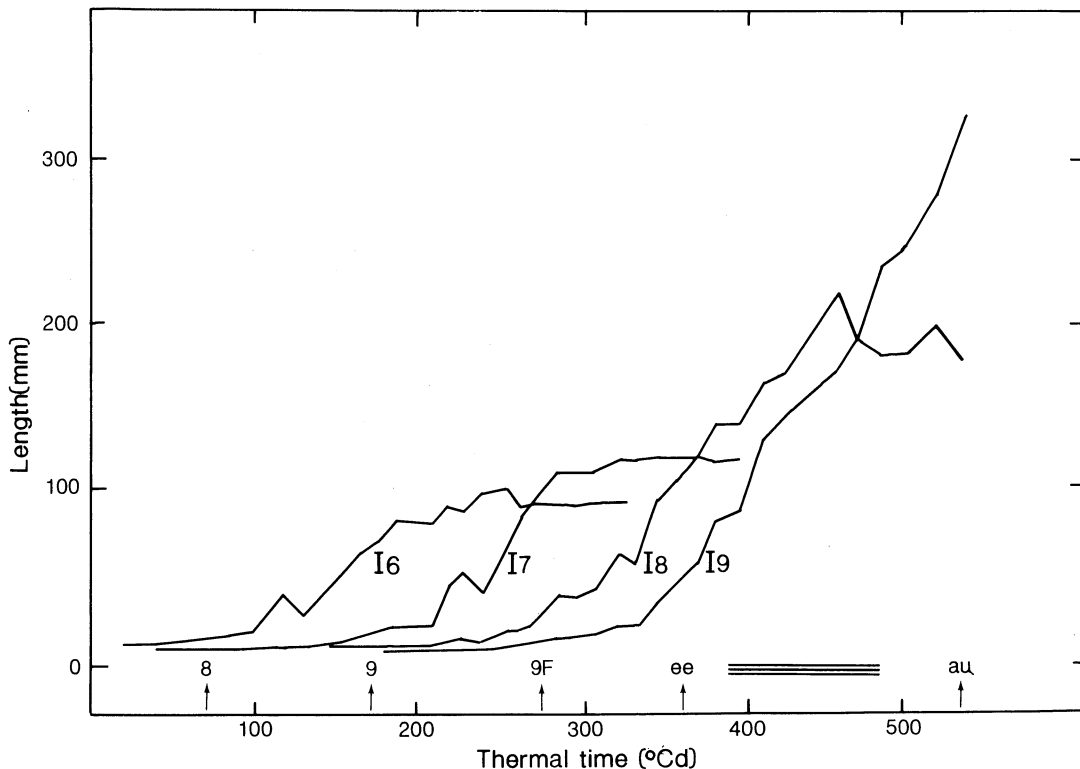
Figure 2. Internode length (16 to 19) versus thermal time. The meanings of the symbols are given in Fig. 1.

matter versus thermal time curve was generally sigmoid, there was a long phase of slow dry matter accumulation before the internode reached its maximum dry mass (Fig. 3).

Modified logistic function curves were fitted to the length (Table 1) and dry mass versus thermal time data for

Table 1. Length growth parameters for modifed logistic function.

	Leaves			
	L6	L7	L8	L9
B		0.020	0.028	0.035
M			103	207
T			1.43	1.89
C		460	451	403

	Internodes				
	16	17	18	19	Ear
B	0.088	0.090	0.039	0.023	0.068
M	159	254	335	447	318
T	3.85	3.98	1.76	1.18	5.71
C	86	116	181	347	100

the leaves, internodes and ear. Analyses of the length curves showed that there was a consistent relation between growth of a leaf and its subtending internode. Each internode reached the inflection point of the growth curve about 150 °Cd after the point of inflection of the growth curve for the leaf. The interval between inflection points of successive internodes was about 100 °Cd.

DISCUSSION

Death of the florets occurred at about the time of maximum growth rate in dry mass of stem and ear and maximum length growth rate of the peduncle (Fig. 4 and Table 2). This occurred some time after the flag leaf was fully expanded, and when the total leaf area of the plant was declining. Floret death occurred when the peduncle was growing most rapidly. Length growth was concentrated in the intercalary meristem where the rapid growth rate could cause resistance to translocation. Therefore the time of floret death is consistent with the hypothesis that during the phase of vigorous stem and ear growth there are insufficient resources to support the potential growth of all these organs. The later initiated smaller florets are less competitive and obtain insufficient material to support their growth.
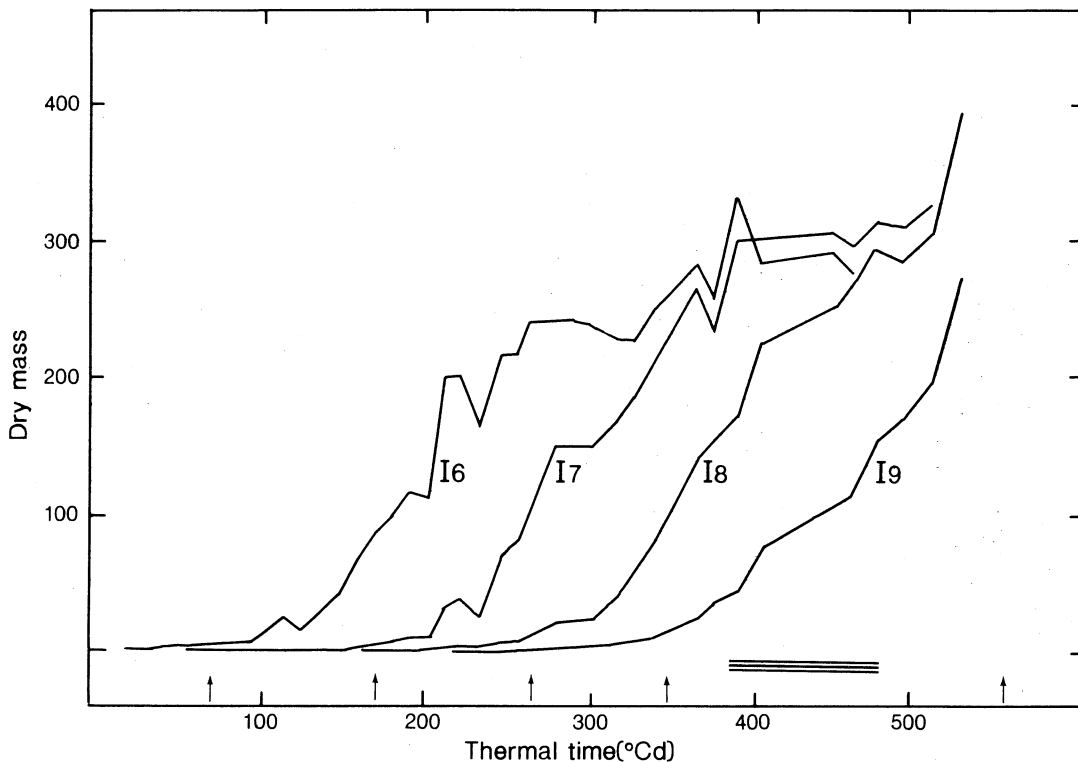
Figure 3. Internode dry mass (I6 to I9) versus thermal time. The meaning of the symbols is given in Fig. 1.

Table 2. The growth rates of I7, I8 and I9 and the ear. The maximum growth rate of the whole stem was 3.8mg/°Cd occurred at 390°Cd.

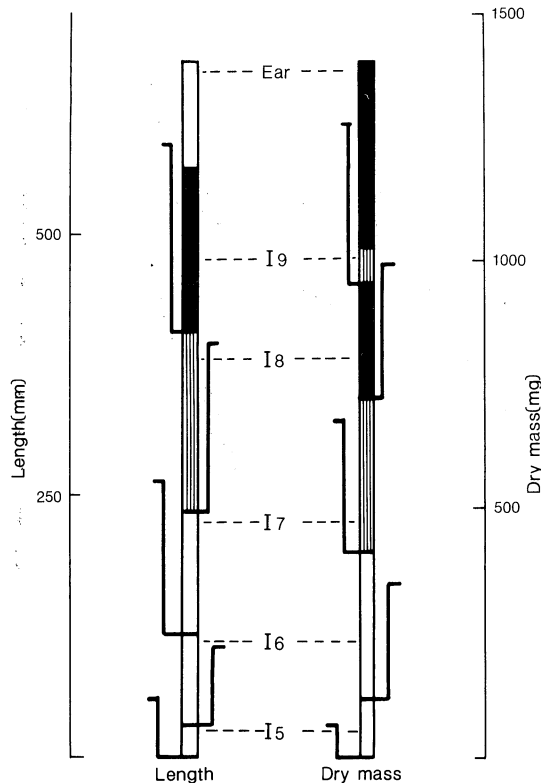|	Length		Dry mass	
	mm/°Cd	% of max	mg/°Cd	% of max
I7	nil	nil	0.7	42
I8	0.5	33	1.7	98
I9	1.9	98	1.0	31
Ear	0.002	1	2.4	85

Table 3. Ratio of stem and ear growth rates in tall (rht2) and semi-dwarf (Rht2) lines. (Brooking and Kirby, 1981).

	Line	Glasshouse	Field
rht2	CD	31.9	29.3
	TT	33.6	32.3
	ST	33.9	34.2
Rht2	HS	45.2	45.5
	SD	42.4	41.0
	TD	37.1	41.1

Changes in radiation during the ear growth phase have been shown to affect partitioning of dry matter to the ear and the number of grains per ear (Fischer, 1985), and Stockman et al. (1983) have shown that shortage of assimilate reduces the number of competent florets per spikelet.

There are genetic differences, particularly due to semi-dwarfing genes, in the partitioning of dry matter between ear and stem. Brooking and Kirby (1981), working with the lines from the progeny of a tall x semi-dwarf (Rht2) cross, found that lines with the Rht2 gene partitioned more dry matter to the ear than did the tall lines (Table 3). This was associated with a greater number of competent florets per spikelet. Similar results have been obtained by Borrell (1985) using lines of Triple Dirk, isogenic for Rht1 and Rht2.

The improvement in yield which has been associated with the use of semi-dwarfing genes may therefore be due to their effect on the partitioning of dry matter between stem and ear, thereby affecting their competitive relationship. Beacuse the timing of floret death indicates that the period of most severe competition is when the peduncle and the penultimate internode are growing most rapidly, further improvement in number of grains per spikelet may result

Figure 4. Length and dry mass and rates of growth of the ear and internodes at the mid-point of floret death (435 °Cd). The coding of the growth rates is as follows: ■ high growth rate (>70% of maximum); ▥ moderate growth rate (>10% <70% of maximum); ☐ low growth rate (<10% of maximum). At this stage all the leaves were fully expanded and were not growing.

from selecting for a reduced peduncle size relative to the other internodes.

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SYMPOSIUM DISCUSSION

Sir Otto Frankel, CSIRO

In past experiments I have seen cases where there are only three grains in the spikelet but none below positions 6 or 7. This would lead to the conclusion that it is not competition from the leaves and stem but from grains lower in the spikelet that controls the formation of grains in the upper spikelet.

Kirby

I have given consideration to your work in drawing my conclusions. However, in the field situation the death of florets has always occurred at the terminal part of the spikelet and in none of these situations did we find any failure to set in the lower grains. I think the test of your hypothesis would come if the genes were put into a background with and without the Rht gene.

Dr A.J. Rathjen, University of Adelaide

Have you considered barley? Being diploid it would be much quicker as far as the flag leaf size and development are concerned.

Kirby

Yes, this work really started off in barley. Now, with the advent of the Rht genes we've got a much better handle to work with in wheat. In barley there is exactly the same phenomenon, but instead of florets dying, the spikelets at the top of the ear die back. There is considerable variation in this.

Prof. K.J. Kasha, University of Guelph

Some years ago I worked with a number of mutants with a long basal internode on the barley spike. To further support your argument, these type of mutants which are simply inherited could often have losses in the tip of the spike.