RATE AND DURATION OF GRAIN GROWTH IN SEVERAL WHEAT CULTIVARS

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INTRODUCTION

Wheat yield variations are associated with many agronomic, genotypic and environmental factors, but the underlying physiological reasons for the variations are usually poorly understood. Grain yields are often described in terms of yield components such as ear population, grains per ear and seed mass. This approach cannot be used to explain how yield varies; it merely describes the structure of seed yield per unit area. Variations can be explained only if the underlying processes which contribute to yield formation are identified and understood. This can be done by developing and using models of crop growth and development as analytical frameworks for examining the causes of yield variations.

This paper describes briefly a simple wheat model and how it was used to analyse and identify the causes of yield variations among intensively managed crops of four contrasting cultivars grown in three seasons. Grain growth rates and durations were measured in all crops, and the model was used to analyse the time courses of grain growth. The paper is a summary only; a detailed description of the project will be published elsewhere.

THE MODEL

The basis of the yield prediction aspect of the model is that yield depends on the rate and duration of grain growth. Hence, a principal objective in developing the model was that it should simulate grain growth rate and duration accurately, accounting for differences among genotypes and for environmental effects.

Duration of Grain Growth

The model assumes that for each cultivar the duration of grain growth is a constant number of degree days, or thermal time units above a base temperature *Tb*, after anthesis. Conversely, grain development rate, the reciprocal of the duration, is related linearly to temperature above *Tb*. Both *Tb* and the number of thermal time units from anthesis to the end of grain growth may differ among cultivars, and must be found experimentally. Unless environmental or management factors reduce it, the chronological duration of grain growth depends on the cultivar and the temperatures it experiences during grain growth.

Grain Growth Rate

Dry matter for grain growth is assumed to come from two sources: new growth during grain fill and translocation from stems and leaves of dry matter produced before anthesis. The daily contribution to grain growth from each source (*Cc* and *Ct* respectively) is calculated separately, and the two summed to obtain the daily growth rate (*Cg*):

$$Cg = Cc + Ct \qquad (1)$$

All new dry matter produced after anthesis is assumed to be grain. The daily crop growth rate (*Cc*) is assumed to be directly proportional to the amount of photosynthetically active radiation (PAR) intercepted by the crop (*Q*). *Q* may be estimated from measurements of incident PAR (*Qo*) and either green leaf area index (*GAI*) or the ratio *Q/Qo*. The proportionality constant (*A*) is the efficiency with which *PAR* is used to produce new dry matter. A radiation extinction constant (*k*) depends on the geometry of the crop canopy:

$$Cc = A\,Q = A\,Qo\,(Q/Qo) = A\,Qo\,(1 - \exp(-k\,GAI)) \qquad (2)$$

A constant proportion (*B*) of above-ground dry matter present at anthesis (*Ma*) is assumed to be translocated into the grain. Assumptions in the model are that *Ct* is related linearly to temperature above the same base (*Tb*) as grain development, and that the duration of translocation is the same as the duration of grain growth. Thus daily *Ct* is calculated as a function of grain growth duration and the amount of dry matter available for translocation (*B Ma*).

MATERIALS AND METHODS

Measurements were made on crops of four cultivars (Avalon, Bounty, Moulin and Rongotea) grown at Lincoln in the 1984-85, 1985-86 and 1986-87 seasons. The crops were sown in May in the first two seasons, and in May, June and July in the third season. All were intensively managed, with high rates of fertilizer applications, regular fungicide applications to achieve good disease control, and irrigations when required according to water budget calculations. Measurements of incident PAR (*Qo*) and daily temperatures were obtained from a weather station near the experimental crops.

Total above-ground dry matter per unit area and Q/Qo were measured at about 2 weekly intervals from emergence and the results used to obtain estimates of A (equation 2). From anthesis, grain dry mass per unit area and *Q/Qo* were measured every 4 to 5 days until the end of grain growth. Estimates of *Ma*, daily *Cg* and grain growth duration were determined from logistic growth curves fitted to dry mass data. The amount of dry matter translocated (*B Ma*) was calculated as the difference between final grain yield and *A Qg*, where *Qg* is the total PAR intercepted during grain growth. From this basic information, daily estimates of *Cc* and *Ct* were calculated.

RESULTS AND DISCUSSION

All grain yields were high, a result of the intensive management, but there were substantial yield variations among seasons, cultivars and, in 1986-87, sowing times. The highest yielding cultivar was Moulin (10.8 t/ha) and the lowest was Rongotea (8.7 t/ha). The first two sowings in 1986-87 produced the highest yields (10.9 and 10.7 t/ha), and the 1984-85 and 1985-86 crops produced the lowest yields (8.5 and 8.0 t/ha).

Analyses of the causes of the yield variations using the model showed that:

- Grain growth duration did not differ among cultivars, although it was longer for the middle sowing in 1986-87.
- There were no differences among either cultivars or seasons in the amount of dry matter present at anthesis (*Ma*).
- There were significant grain growth rate (*Cg*) differences among both cultivars and seasons.
- Grain yield was highly correlated (r^2 = 69%, 18 d.f.) with the total amount of PAR intercepted during grain growth (*Qg*). The regression had a large positive intercept.

These results mean that the yield variations were associated mainly with variations of grain growth rate rather than duration, and that much of the rate variation was associated with differing amounts of PAR intercepted. Further examination of what was causing *Cg* to vary showed that:

- PAR use efficiency (A) was the same for all cultivars, but it was significantly lower in 1984-85 and 1985-86 than in 1986-87.
- The final yield always exceeded the amount of new dry matter produced during grain growth (*A Qg*), but was highly correlated with it (r^2 = 78%, 18 d.f.).
- *Cg* variations were mainly associated with *Qg* differences.
- All the additional yield was assumed to come from translocation of dry matter present at anthesis (*Ma*). The analyses showed that the proportion of Ma translocated (*B*) was 20% (S.E. = 1%).

After these analyses, the thermal duration of grain growth and the parameters *A* and *B* were assigned constant values in the model for all cultivars. Simulations then gave predictions of grain dry masses and growth rates which were agreed closely with measured values. A regression of predicted versus measured yield had a slope of 1.00 and an r^2 of 72% (18 d.f.).

The next step was to examine solar radiation data to identify any differences of radiation availability to cultivars during grain growth. There were none, although there were significant differences among the seasons. This suggested that *Qg* differences had to be associated with differences among cultivars in their capability to intercept incident radiation. Therefore, the proposition was examined that the patterns of canopy senescence differed among the cultivars, even though the durations of senescence were the same. A ground cover duration (*GCD*), analagous to leaf area duration, was defined as the sum of the daily values of *Q/Qo* from the beginning to end of grain growth, and its variation was tested. This analysis showed that:

- There were significant differences in *GCD* among both cultivars and seasons.
- Grain yield was highly correlated with *GCD* (r^2 = 51%; 17 d.f.).
- A regression of grain yield versus the product of GCD and mean daily incident PAR during grain growth (approximating PAR intercepted) was a significant improvement (r^2 = 70%; 17 d.f.).

Therefore, cultivar yield differences were associated mainly with *GCD* variations. Additional seasonal differences were associated with variations of radiation availability.

CONCLUSIONS

The simple model provided a description of principal grain growth processes which was an excellent framework for analysing the underlying reasons for grain yield variations among cultivars and seasons. Yield variations in these experiments were mainly caused by different amounts of PAR interception by the crops from the beginning of grain growth. Further analyses showed that although the chronological and thermal durations of grain growth were similar for all cultivars and seasons, different patterns of canopy senescence led to different ground cover durations. These were the main causes of variations of intercepted PAR, and hence of grain yield.