

# A NEW MODEL OF SPRING WHEAT PHENOLOGICAL RESPONSE TO TEMPERATURE AND DAYLENGTH

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*Summary.* The development of spring wheat in response to temperature and daylength may be likened to the operation of an alarm clock. The clock rate, the external expression of which is the successive appearance of leaves, depends only on the temperature of the apex and the number of leaves present. The alarm, expressed as the fixing of final mainstem leaf number, is set by a response to daylength some time after emergence. Anthesis and the start and finish of grain growth follow the appearance of the flag leaf ligule at fixed thermal time intervals. This model implies that the development of the apex beyond the appearance of the flag leaf primordium has no impact on the timing of anthesis. Our experimental evidence supports the model. The time of response to daylength in responsive cultivars is delayed sufficiently that autumn-sown plants develop more leaves than spring-sown plants of the same cultivar emerging into the same daylength.

## INTRODUCTION

The difficulty in predicting anthesis date is a major cause of the failure of simulation models to predict grain yield correctly (1). This is largely because the timing of anthesis determines the part of the season during which the grain will grow. The timing of anthesis responds to sowing time through influences of temperature and daylength on the duration of phases before anthesis. Most models of responses of spring wheat development to daylength and temperature calculate the duration of phases in thermal time, with adjustments that vary the duration according to daylength through the concept of photothermal time (2). The phases chosen are between events that can be observed on the apex of the mainstem, *viz.* seedling emergence, double ridge formation, terminal spikelet, and anthesis. It has been suggested that daylength may affect the thermal durations of these phases in a complex manner (3). However, a major reason for the apparent complexity is that the chosen scale has only a loose connection with developmental mechanisms.

A better approach is to consider development of the mainstem in wheat as the sequential appearance of primordia, and then their differentiation into the structures that they will become. Lower primordia will become leaves, and upper primordia spikelets. Except in very unusual conditions, leaves never form above spikelets. Once some of the upper primordia commit themselves to being spikelets, then the plant will inevitably flower, because some primordium below this level will be the flag leaf. Leaf appearance is closely coordinated with the formation of primordia on the apex (4). Thus, the most important biological events that determine the timing of anthesis are the formation of the flag leaf primordium, the appearance of the flag leaf, and the duration of the interval between flag leaf appearance and anthesis. The advantage of this description is that it explains logically why durations vary. Primordia appear at a rate determined by environmental factors, and phase durations depend both on this rate and the number of primordia formed. Hence the timing of double ridges and terminal spikelet, events that are solely associated with the early development of the ear, are not needed to determine the timing of anthesis.

A more mechanistic model uses the rate of appearance of leaves, the number of leaves, and the responses of these to daylength and temperature (5, 6) to determine the timing of anthesis. In this paper we report on the development of such a model based on measurements and analysis reported elsewhere (7, 8).

## MATERIALS AND METHODS

Experimental data on leaf appearance for model development were obtained in 1984 from four sowings of *cv. Avalon* wheat at Palmerston North, New Zealand (latitude 40.2°S, longitude 171.8°E), and for model validation from four sowings of *cv. Rongotea* wheat at Lincoln, New Zealand (latitude 43.6°S, longitude 172.3°E). Sowing dates at Palmerston North were 11 May, 1 June, 21 September and 2 November; and at Lincoln they were 4 May, 13 June, 1 August and 12 September. All crops received sufficient water and fertiliser to avoid significant stress (1, 9).

At Palmerston North, five plants were harvested at approximately seven-day intervals from emergence, and the Haun stage determined (number of visible ligules plus the fraction of the next emerging leaf (10)). Hourly mean air and soil temperatures were logged - air temperature using a screened thermistor above the canopy, and soil temperature using a thermistor at 2 cm depth. At Lincoln, the mean time of ligule appearance was determined from regular observations of 10 tagged plants in each plot. All climatic data at Lincoln were collected from a weather station approximately 300 m from the experiment site.

To determine response of leaf number to daylength, six sowings of 11 wheat cultivars were made at approximately two-month intervals from 2 June 1989 and to 5 April 1990 at Palmerston North (7). Of these, four cultivars (Batten, Rongotea, Otane and CRSW6) with no vernalisation requirement (7) were chosen for analysis of daylength response. Plots were sown at populations of 300 plants/m<sup>2</sup> and were provided with adequate water and fertiliser. At 10 to 15-day intervals throughout the season, 15 plants per cultivar were harvested and the Haun stage determined (10). The plants were then dissected and the number of primordia counted, cumulative from leaf 1. The final number of mainstem leaves ( $L_f$ ) was determined at flag leaf emergence as the mean number of leaves per mainstem. Non-integer  $L_f$  values reflect the fact that in most cases, although most plants had a similar leaf number, there were almost always a few plants with either one more or one less leaf.

A model was developed from the measurements in the two Palmerston North experiments. Validation of final leaf number predictions were made by comparison with measurements from the experiment at Lincoln (above). Validation of predictions of anthesis date were made using data from other experiments at Lincoln (1).

## RESULTS AND DISCUSSION

When the Haun stage in the first Palmerston North experiment was plotted against thermal time (base 0°C) using air temperature (Fig. 1a), the data separated into a lower "winter" rate for the early sowings, and a faster "spring" rate for the later sowings (8). Phyllochrons, calculated as the reciprocals of the rates for the first eight leaves, were 93 and 72°C days/leaf respectively. However, a similar plot using temperature near the apex showed that a single relationship described all the data (Fig. 1b), with a phyllochron of 89°C days/leaf (8). This finding suggests that leaf appearance responds to the temperature of the apex; there is no need to appeal to a preconditioning response to such factors as rate of change of daylength to explain differences between the phyllochrons of autumn and spring sown crops (11).

Plots of final mainstem leaf number from the second Palmerston North experiment against daylength at Haun stage 1.5 showed considerable hysteresis, with plants emerging into decreasing daylengths setting more leaves than those emerging into increasing daylengths (Fig. 2a). For Rongotea, the hysteresis persisted when the daylength occurring at the time the final leaf primordium (FLP) was set was used (Fig 2b). The hysteresis disappeared only when either mean daylength for the period FLP to terminal spikelet was used (Fig 2c) or that for two leaves past the time of FLP (Fig 2d). Cultivar differences were apparent. Batten behaved similarly to Rongotea, but the results for Otane were without hysteresis at FLP, and for CRSW6 not until four leaves past FLP.

We assume that, when the relationship between final leaf number and daylength is linear and without hysteresis, we have established the correct timing of the response to daylength. This is the simplest hypothesis, and means that the plants are responding to an immediate stimulus (daylength only), without a mechanism to distinguish spring from autumn, or lengthening from diminishing days. The rate of change of daylength has no influence on final leaf number independent of the effects of daylength (12).

In two of the four cultivars that we analysed, final commitment of the last leaf primordium was controlled by the daylength midway through spikelet initiation. In the third and fourth cultivars, the daylengths at the beginning and end respectively of the spikelet initiation phase were the controlling factors. Only Otane showed evidence of a saturation response to daylength, i.e. a daylength beyond which final leaf number was no longer reduced.

The results suggest that cultivars differ in the timing of their response of final leaf number to daylength, as well as in the magnitude of their response. There is obviously a response to daylength before the final leaf number is fixed, because the point of intersection on the relationship between leaves and primordia occurs within a few primordia of the first spikelet primordium (13). However, the final leaf primordium may not be committed to being a leaf until many plastochrons after it has formed. Indeed, this commitment may not occur until after terminal spikelet (14). Otane, which responds to daylength either at or slightly before the initiation of the first spikelet primordium, is unlikely to have many labile primordia. In contrast, CRSW6 sets its final leaf number close to when it forms its terminal spikelet. Therefore, it can have several primordia that may become either leaves or spikelets, depending on their position and the daylength at terminal spikelet.

#### A MODEL FOR PREDICTING FINAL LEAF NUMBER AND ANTHESIS DATE

The results of the analysis above were incorporated into the wheat simulation model *Sirius* (7,8). Leaf appearance is calculated from a response of leaf appearance rate to temperature and leaf number using simulated soil temperature until Haun stage 4 and simulated canopy temperature thereafter (8). Primordium appearance is calculated from the relationship of primordium number to leaf number (7). Daylength is calculated first at Haun 1.5, and used to estimate the likely leaf number at which the stage of commitment will be reached. The calculation is updated at half leaf intervals until this stage is reached, and the final leaf number is then determined. Anthesis is assumed to occur three phyllochrons after the appearance of the flag leaf ligule (7).

The model was able to predict final leaf number for cultivar Rongotea at Lincoln for four sowings with a root mean square deviation (RMSD) of 0.2 leaves, and the anthesis date for the same sowings with an RMSD of 3.2 days. Model predictions of anthesis for Rongotea from all the Lincoln experiments (1) had an RMSD of 4.6 days, considerably improved over the estimates from AFRCWHEAT2 (6.5 days) and CERES-Wheat (22.3 days).

#### CONCLUSIONS

The response to daylength of final leaf number in spring wheat plants is an adaptation that increases their longevity if they emerge in short days in winter or very early spring. Also, because the final leaf number is fixed so late, the adaptation extends longevity even further if they emerge in autumn. Finally, it provides a mechanism for synchronising anthesis among plants in the same field by compensating for different leaf emergence rates, associated with small variations in environment, by allowing adjustment of the final leaf number. The model presented here requires that the plants respond only to their immediate environment. They do not require any preconditioning to synchronise flowering, and especially do not require any mechanisms for distinguishing lengthening from diminishing daylengths.

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