

How temperature and daylength determine flowering time in spring wheat - a discussion

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Abstract

Wheat develops by accumulating primordia on the apical meristem, and then differentiating them into the structures they will become. Leaf and primordium appearance are coordinated during early development. Anthesis occurs a constant thermal time interval after the ligule of the flag leaf appears. A mechanistic model of wheat development uses this framework to describe the effects of temperature and daylength on the timing of anthesis. From recently published work, we demonstrate that the main effect of temperature is to control the rate at which primordia and leaves are produced, and the main effect of daylength is to control their numbers. The response to daylength continues until some time after the flag leaf primordium is formed, so that commitment of that primordium, and hence the fixing of final leaf number, can be as late as the terminal spikelet phase in some cultivars. The time of sensitivity to daylength is delayed sufficiently that autumn-sown crops develop more leaves than spring-sown crops of the same cultivar emerging into the same daylength.

Introduction

The timing of phenological events in wheat, particularly anthesis, is an important determinant of performance. This is because the timing of anthesis determines the part of the season in which grain will grow. Cultivars and management choices such as sowing date are chosen so that grain will grow in the most favourable part of the year. Porter *et al.* (1993) identified failure to predict anthesis date correctly as a major cause of the failure of simulation models to give correct predictions of yield.

Wheat crops are usually adapted to the conditions in the locale where they were developed, and are able to synchronise their times of flowering in response to variations in sowing time through responses to daylength and temperature (Hay and Kirby, 1991). Several current models incorporate descriptions of phenological responses to temperature and daylength (e.g., AFRCWHEAT2, Porter 1993; CERES-Wheat, Ritchie and Otter, 1985). Phenophases are defined between observable states of the plant or the apex, *viz.* seedling emergence, double ridges, terminal spikelet and anthesis. Phase durations are assumed to be constant in thermal time (so account for direct temperature effects), but the accumulation of thermal time is reduced in short days, or

where vernalisation is incomplete (the latter accounts for indirect temperature effects). Recently Slafer and Rawson (1994a) reviewed current knowledge on effects of temperature and daylength, and concluded that although daylength and vernalisation had no influence on the durations of pre-emergence or post-anthesis phases, their effects were not confined to the vegetative development phase of the apex (pre-double ridges), but continued to influence post-floral development. A major conclusion was that wheat development is too complicated to be accounted for by simple models. A further implication was that responses during the various phenophases may be controlled by different genes, and that there was scope for manipulation or selection of these to influence phenotype.

A reason for the conclusions above is that the framework used for analysis is only loosely linked to developmental mechanisms. There is little link between the responses described and the processes that cause them. An alternative mechanistic framework is a description of main stem development 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 (unless it dies), because some primordium below this level will be the flag leaf. Leaf appearance is closely coordinated with the formation of primordia on the apex (Kirby, 1990). The most important biological events that determine the timing of anthesis are then 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 framework is that it describes why the durations vary. Primordia appear at a rate determined by environmental factors, and phase durations depend both on this and the number of primordia formed.

How does this framework relate to the more traditional approach used by Slafer and Rawson (1994a)? Floral initiation is defined as the appearance of the first spikelet primordium. At about this time there is a sharp increase in the rate of primordium production (Kirby, 1990). The double ridges stage is the first visible sign that some spikelet primordia are committed (Brooking *et al.*, 1995), but can occur when from 20-80% of spikelet primordia have been formed (Delécolle *et al.*, 1989). Therefore it is not well associated with floral initiation, as often assumed (Slafer and Rawson, 1994a). The terminal spikelet occurs when all spikelet primordia have been formed. Double ridges and terminal spikelet are events that are solely associated with the early development of the ear. Their timings are not necessary steps in the calculation of the timing of anthesis. This remains true even if the first spikelet primordium is not committed as such until some time after it is formed (Brooking *et al.*, 1995).

Implications of the alternative scale

Kirby (1990) found a fixed relationship between primordium (P) and leaf (L) numbers up until about floral initiation for a large range of cultivars and conditions. A similar relationship was reported by Brooking *et al.* (1995), with the wheat cv. Avalon. To a reasonable degree of approximation, this can be written:

$$P = 2L + 4 \quad (1)$$

Therefore, the number of leaves L_x left to emerge when the flag leaf primordium is formed (i.e when $P=L_r$, the final leaf number), is directly proportional to the leaf number (L_p) at that time:

$$L_x = L_r - L_p = L_p + 4 \quad (2)$$

This means that any apparent responses in the duration of post-floral phenophases to vernalisation or photoperiod are through the effect on leaf number, especially if the thermal duration of the phase from flag leaf ligule appearance to anthesis is constant for a cultivar (Amir and Sinclair, 1991). Assuming that the phyllochron (T_{phyll}) for leaves occurring after floral initiation is constant in thermal time, and that anthesis occurs about three phyllochrons after the appearance of the flag leaf ligule (Jamieson *et al.*, 1995), the thermal time (T_{flan}) from floral initiation to anthesis is:

$$T_{\text{flan}} = T_{\text{phyll}}(L_x + 3) \quad (3)$$

In other words, the duration of the interval from floral initiation to anthesis will depend both on temperature and any factor (e.g vernalisation or daylength) that influences final leaf number.

Equations 2 and 3 provide some further evidence that double ridges is not a good indicator of the end of the vegetative phase. Hay (1986) found that for a series of sowings of wheat at Auchincruve, U.K., anthesis occurred over a very short time span: the duration of the phase from sowing to anthesis was linearly and negatively correlated with the delay in sowing after July. Most of the variation was associated with changes in the duration of the phase from sowing to double ridges, and the phase double ridges to anthesis was nearly constant, with one exception where the first phase was substantially expanded. Necessarily, much of the variation must have been associated with changes in final leaf number. Therefore, according to equation 3, a substantial part of the variation, not directly associated with temperature, was necessarily associated with changes in the duration of the post-vegetative phase. Hence, the relationship between the occurrence of double ridges and floral initiation must have changed systematically to account for the observations. The occurrence of an outlying point is not unexpected.

The result of the above argument is that any model that considers only response of the durations of phenophases to environmental factors is likely to fail once outside a narrow range of sowing times. Because the intermediate stage of double ridges is a moving target, it is also likely to imply that processes are more complex than they are. A sounder model is based on responses of the underlying mechanisms. That is, primordia and leaf production rates and numbers, to variations in environment.

In this paper we use the above framework to demonstrate the nature and timing of the response of phenological development in spring wheat cultivars

(those with no response to vernalisation) to daylength and temperature, based on analyses recently published by Jamieson *et al.* (1995) and Brooking *et al.* (1995). The analysis is based on two hypotheses:

1. Leaf appearance rate depends only on the temperature of the apex and the current Haun stage (Haun, 1973), and is independent of daylength or its rate of change.
2. Final main stem leaf number (FLN) depends on daylength at some time after emergence.

These hypotheses imply that interactions between daylength and temperature will occur because temperature will determine the daylength to which the plants will be exposed.

Temperature effects on leaf production

An important part of hypothesis 1 is that it is based on responses to temperature at the apex, with no implicit assumption that this is the same as air temperature. There are many observations suggesting that leaf appearance rates vary with sowing time (Baker *et al.*, 1980; Masle *et al.*, 1989; Hay and Delécolle, 1989). This has led to a number of models that assume some preconditioning of the leaf appearance rate in response to daylength (Cao and Moss, 1991) or its rate of change at or near emergence (Baker *et al.*, 1980). However, Jamieson *et al.* (1995) showed that, even though leaf production rates in thermal time were different for autumn and winter sown plants than for spring sown plants when thermal time was calculated from air temperature (Fig. 1a), the differences vanished when the thermal time was calculated from soil temperature until stem elongation began, and thence on air temperature (Fig. 1b). They also showed that a model that simulated soil and canopy temperature predicted leaf appearance much more closely than models based on air temperature alone, or on air temperature adjusted for rate of change of daylength at emergence. This, therefore, supplies the basis for describing temperature responses.

Daylength effects on final main stem leaf number

In spring wheats, i.e., those where $t \geq 20$ July 1996 there is no response to vernalisation, temperature has no direct effect on FLN (Slafer and Rawson, 1994b). Wheat is a long day plant, and in responsive cultivars, more leaves are set when the early development is in short days than when in long. A model of FLN response to daylength

was developed by Miglietta (1991). It assumed that FLN was fixed almost immediately after seedling emergence. It was successful in predicting FLN and anthesis date for a range of locations, provided sowing dates were within the conventional range. However, Brooking *et al.* (1995) showed that FLN is not necessarily fixed until well after seedling emergence and, in some case, until considerably after the flag leaf primordium is formed. They analysed the response to daylength of four spring cultivars (Batten, Otane, Rongotea and CRSW6) sown at two-month intervals over an annual cycle at Palmerston North. This meant the plants were exposed to a wide range of daylengths during early development

An example of the analysis is shown in Figure 2 for cv. Rongotea. Plots of final main stem leaf number 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). The hysteresis persisted when the daylength occurring at the time the final leaf primordium (FLP) was formed 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.

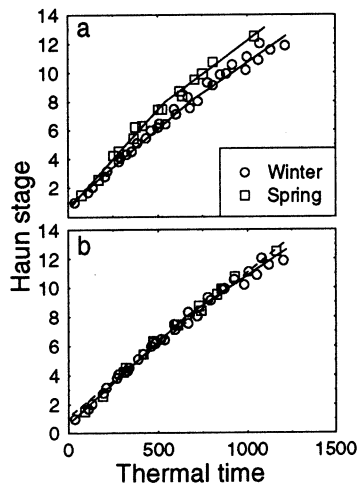


Figure 1. Plots leaf numbers of Avalon wheat at Palmerston North against thermal time calculated from (a) air temperature and (b) apex temperature.

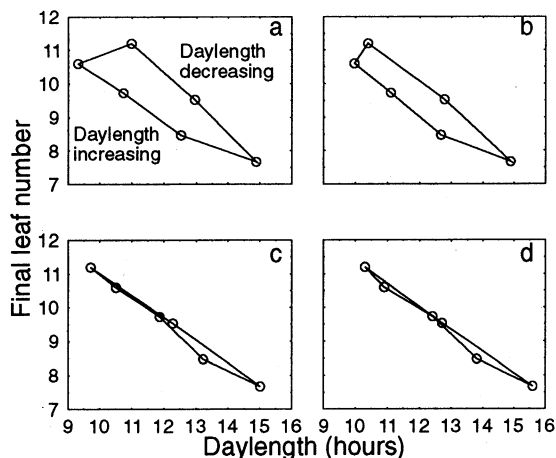


Figure 2. Final leaf number in Rongotea wheat versus daylength at (a) Haun 1.5, (b) FLP, (c) Mean of FLP and terminal spikelet and (d) FLP plus 2 leaves.

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 hypothesis is much simpler than those that require a mechanism to distinguish spring from autumn, or lengthening from diminishing days, and means that the plants are responding to an immediate stimulus (daylength only). The rate of change of daylength has been shown to have no influence on final leaf number independent of the effects of daylength (Slafer *et al.*, 1994).

In two of the four cultivars analysed, final commitment of the last leaf primordium was controlled by the daylength midway through spikelet initiation. In the third and fourth cultivars, final leaf numbers were set in response to the daylengths at the beginning and end respectively of the spikelet initiation phase. Only cv. 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 change in slope of the relationship between leaves and primordia occurs within

a few primordia of the first spikelet primordium (Hay and Delécolle, 1989). 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 (Hutley-Bull and Schwabe, 1980). 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

That the timing of daylength response is after, but associated with, the production of the flag leaf primordium creates its own special problems in prediction. On the surface, it appears that knowledge of the event to be predicted is required to predict it. This can be and has been overcome by sequential sampling of daylength and iterative calculations of FLN. The process is described below.

Formalised descriptions of leaf appearance rate response to temperature and FLN response to daylength were incorporated into the wheat simulation model *Sirius* (Jamieson and Wilson, 1988; Jamieson, 1989). In the model, leaf appearance is calculated using simulated soil temperature until Haun stage 4 and simulated canopy temperature thereafter (Jamieson *et al.*, 1995). Primordium appearance is calculated from the relationship of primordium number to leaf number (Brooking *et al.*, 1995). Daylength at Haun 1.5 is 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 (Brooking *et al.*, 1995).

The model was able to predict final leaf number for cv. 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 (Brooking *et al.*, 1995). Model predictions of anthesis for Rongotea from other Lincoln experiments (Porter *et al.*, 1993) 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. Because the final leaf number is fixed so late, the adaptation extends longevity even further if they emerge in autumn. In addition, 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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