



Phenological response of spring wheat to timing of photoperiod perception: The effect of sowing depth on final leaf number in spring wheat



E.D. Meenken^{a,b,*}, H.E. Brown^a, C.M. Triggs^b, I.R. Brooking^c, M. Forbes^a

^a The New Zealand Institute for Plant & Food Research Limited, Private Bag 4704, Lincoln, 7608, New Zealand

^b The New Zealand Institute for Plant & Food Research Limited, Private Bag 4442, Palmerston North, New Zealand

^c The University of Auckland, Department of Statistics, Private Bag 92019, Auckland, 1142, New Zealand

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ABSTRACT

Wheat phenological modelling literature suggests final leaf number (FLN) targets of wheat (*Triticum aestivum*) will be set only once daylight is perceived and will be based upon environmental and cultivar-specific genetics at that time. Development is thought to proceed relative to thermal time regardless of light perception prior to emergence. Modelled predictions of final leaf number (FLN) and thence anthesis are based on this mechanism. Results did not support this hypothesis, and we suggest an alternative hypothesis based on molecular interactions between vernalization genes *Vrn1*, *Vrn2* and *Vrn3*.

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1. Introduction

The final number of leaves (FLN) attained by a wheat plant is an important property that determines the timing of anthesis (Hay and Porter, 2006). This can influence timing of when the plant becomes reproductive, and hence have a major impact on yield. For example, in Australia, delays in sowing, and hence in timing of anthesis, can represent substantial yield losses of between 7 and 17% per week (Rebetzke et al., 2007) and in Japan ca. 3% per day (Tanio and Kato, 2007).

Current phenological models describing progress toward anthesis focus on mechanisms that occur during the vegetative stage between emergence and flag leaf (FL) appearance. Developmental progress in the period between imbibition and emergence is modelled as a constant relationship between organ (primordia)

numbers and accumulated Tt (Brooking et al., 1995). We aim to determine the extent of uncertainty that is introduced to the modelling of FLN by assuming this constant developmental progress prior to emergence.

1.1. Wheat development between emergence and anthesis under phenological model SIRIUS

The process-based phenological development mechanisms incorporated into the wheat model SIRIUS (Jamieson et al., 1998) provide a link between vegetative development (leaf appearance) and the switch to reproductive development. Key early phases of development in a wheat plant include: a) imbibition, when the grain absorbs moisture, begins to develop primordia and the apex extends; b) emergence, when the plant first perceives light; c) vernalisation saturation, when winter varieties are able to respond to photoperiod; d) floral initiation, or reproductive commitment, when the plant switches from vegetative to reproductive development; and e) terminal spikelet (TS), the final organ to be initiated prior to biomass sequestration phase.

* Corresponding author at: The New Zealand Institute for Plant & Food Research Limited, Private Bag 4704, Lincoln, 7608, New Zealand.

E-mail address: esther.meenken@plantandfood.co.nz (E.D. Meenken).

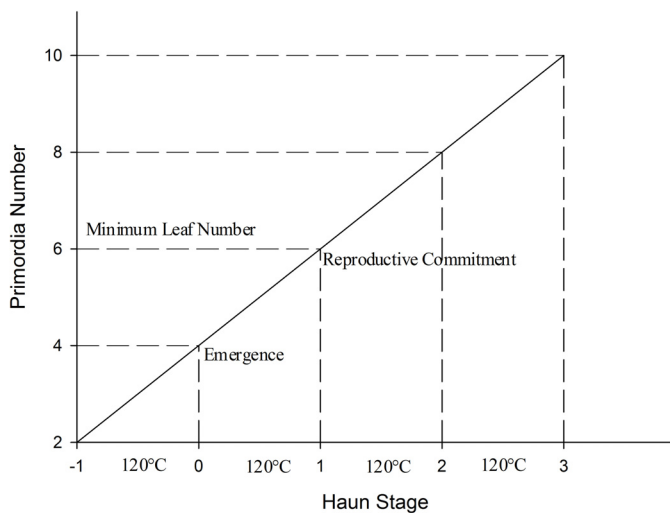


Fig. 1. Sequence of development of primordia in Tt and their relationship to Haun stage. The scale on the x-axis between -1 and 0 represents the period after imbibition but prior to apex emergence when additional primordia have begun to develop but the apex has not yet begun to extend the first leaf.

The development of primordia in thermal time (Tt) as conceptualised in SIRIUS for spring wheat varieties is shown in Fig. 1. Spring wheat varieties are traditionally defined as those that do not require a period of cold temperatures of around 0 – 10 °C (vernalisation) to flower. After emergence, the plastochron, time taken for a primordium to develop, is closely linked to the phyllochron, time taken for a leaf to develop, and the general rule of thumb is that there are two plastochrons to one phyllochron. Therefore, since the phyllochron up until the 2nd Haun stage (Haun, 1973) is approximately 120° days, the plastochron prior to emergence and during the first two Haun stages should be approximately 60° days. At emergence, most spring wheat cultivars require around 1–2 Haun Stages (~ 240 accumulated degree days) before they become able to respond to photoperiod (Brooking et al., 1995). If the photoperiod (Pp) is saturating (approximately 16 h) when the plant becomes responsive to Pp, then the conditions are said to be fully inductive and the plant sets FLN at the number of primordia developed at that time (usually 6–8). At the same time, the plant commits to becoming reproductive (Brooking and Jamieson, 2002).

1.2. Wheat development prior to emergence

In SIRIUS, developmental progress in the period between imbibition and emergence is modelled as a direct, constant relationship between primordia numbers and accumulated Tt (Brooking et al., 1995). The number of primordia at emergence (PAE) is fixed at a constant value of four (Fig. 1). It is made up of two primordia which are present on the main-stem in the seed, and a further two primordia that are initiated between germination and emergence, assuming one phyllochron from imbibition to emergence. This is appropriate for a sowing depth of approximately 5 cm (Kirby et al., 1987; Kirby, 1993; Hay and Porter, 2006). Since the SIRIUS mechanism requires that primordia number (PN) increase in time and directly influence FLN, it can be hypothesised that deeper sowings will give later emergence, and a higher PAE. PN will then increase at 2° LN from emergence until commitment. Assuming long days, the plant will set its FLN based on PN at $\sim 240^\circ$ days after emergence (as seen in Fig. 1). This is based on a base temperature of 0° . This number will be greater if the plant was sown deeper and took longer to emerge. Thus deeper sowing would cause a higher FLN.

To determine the extent of uncertainty that is introduced by assuming PAE is constant, the effect of sowing depth on a) FLN, b)

the number of primordia present at emergence, and c) timing of emergence will be explored.

The following hypotheses were tested in a set of three glasshouse based trials:

1. Does sowing depth affect timing of emergence and FLN in spring wheat varieties?
If yes, then we need to confirm development is progressing as expected:
2. Does later light perception lead to greater numbers of primordia? Finally, can we relate these two, such that:
3. Given expected development in response to Tt prior to Pp perception (emergence) occurs, does extended development time prior to Pp perception increase or decrease FLN?

2. Materials and methods

2.1. Glasshouse and incubator growing conditions

The growing medium for all trials excepting the petri dish treatment in Trials two and three was as follows: 0.3 of a cubic metre of medium was made up of 5 parts crushed bark to 2 parts washed crusher dust. To this was added 1 kg domite lime, 600 g garden lime, 1 kg oscmocote (8–9 months), 350 g super phosphate, 150 g zeolites and 20 g calcium nitrate. The containers had dimensions as follows: Diameter at mouth of pot 19 cm, diameter and base of pot 14 cm, height 19 cm. Glasshouse lighting was set to a photoperiod of 16 h, so that all seedlings emerged into fully inductive conditions. The medium for the petri dish treatment was well soaked cotton wool.

The lighting for all Glasshouse trials was provided by EYE Mercury Lamps HF 400PD, with approximate 1 lamp per square metre. Pots were arranged directly adjacent in the layouts described for each trial. At the start of each trial pots were wetted to field capacity and placed on benches where they were able to drain freely. Thereafter pots were monitored daily and watered to ensure adequate moisture for germination and developmental processes. The daily mean temperature in the glasshouse for the trial period was 15 °C.

Both phytochrome and cryptochrome light reception systems were stimulated using a PHILIPS 28 W halogen lightbulb with an output of 346 lumens. This provides a photoperiod photo flux density of approximately $140 \mu\text{mol}/\text{m}^2/\text{s}$. The temperature in the incubator was held constant at 22 °C. Humidity and moisture were maintained by wetting the growth medium and covering each unit.

2.2. Pilot: genetic ability to emerge from deep sowing in six spring wheat varieties

First a selection of suitable cultivars and sowing depth for each trial was identified in a pilot study. The pilot trial investigated three depths (5.0, 10.0, 15.0 cm) with only 1 replicate pot sown with 15 untreated grains for each cultivar. The six cultivars were 'Otane', 'Kohika', 'Torlesse', 'Spring Batten', 'Morph' and 'Monad'. These varieties were selected as they are commonly used commercial spring wheat cultivars New Zealand. The results recorded from this trial were simply number of seedlings emerged in each pot.

Most grains germinated, regardless of cultivar or sowing depth. Grains sown at 5.0 cm successfully reached the surface; however, most grains sown at 10.0 and 15.0 cm failed to reach the surface. 'Spring Batten' was the exception, exhibiting 60% successful emergence at 10 cm, but only a few plants overall emerged from 15 cm. Haplocotyls that were viable (coleoptile extended at least 1 cm) but did not reach the surface appeared to do so due to lack of sufficient vigour, with the coleoptile extending several cm toward the surface but failing to emerge. The lack of emergence of grains at sowing

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