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Simulation of wheat ontogenesis. II. Predicting dates of ear emergence and main stem final leaf number

F. Miglietta

I.A.T.A.-CNR, Institute of Environmental Analysis and Remote Sensing for Agriculture, P.le delle Cascine 18, I-50144 Florence, Italy

ABSTRACT: The role of photoperiod in the regulation of wheat development and of the final main stem leaf number was studied on the basis of published data from several laboratory experiments. A procedure was developed to calculate the final leaf number and the date of heading of plants that do not require vernalization. Differences between calculations and field observations were ascribed to an effect of vernalization. Hence a model to predict the final number of leaves and date of heading of a given wheat variety was formulated. The model involves the following assumptions: (1) wheat varieties have different sensitivities to daylength; (2) wheat varieties that require vernalization can be vernalized at a very early stage of growth if sown at the beginning of the coldest period of the year; (3) wheat varieties that are vernalized at a very early stage of growth immediately respond to external photoperiodic conditions; (4) wheat crops sown within a range of sowing dates tend to synchronize time of flowering. It was concluded that if the final main stem leaf number of a crop sown at a given date is known, the date of heading and the corresponding final number of main stem leaves of every other sowing can be found. The model was validated using field data from 58 experimental trials performed in the USA and Europe.

INTRODUCTION

By re-interpreting the results of several experiments under controlled conditions and in the field, a model of wheat leaf appearance was developed (Miglietta 1989, 1991). For this purpose, it was shown that the rate of leaf initiation on the main stem depends on temperature and that it is independent of both daylength and rate of change in daylength. This was demonstrated as a consequence of the observation that the length of the period from leaf initiation to appearance increases linearly with increasing leaf number (Miglietta 1991).

An attempt is made in this paper to predict the number of leaves formed on the main stem and the time of final leaf (flag leaf) appearance which is almost independent of the date of sowing in temperate climates (Titta 1934, Van Dobben 1947, Pfeiffer 1949, Orsi 1953, Pal et al. 1959, Henriksen 1961, Shulze & Zabel 1962, Lovato & Amaducci 1965, Tandoi 1967, Vez 1974, Collald 1984, Photiades & Hadijchristodoulou 1984, Green & Ivins 1985, Mucci et al. 1985, Tuttobene et al. 1985, Reinink et al. 1986, Kirby et al. 1987).

This so called 'synchronization' is attributed to a combined effect of vernalization, photoperiod and temperature, and its discovery simplifies to a large extent the problem of prediction of the final number of leaves. In fact, it suffices to calculate the final leaf number for a well-chosen sowing date in order to predict, on the basis of more or less perfect synchronization, the final leaf number of any other sowing.

Here, a model is proposed to evaluate the final number of main stem leaves of any wheat variety sown at any date and latitude under any weather conditions and to calculate the date of flag leaf appearance and the date of heading, which occurs immediately after the flag leaf is fully emerged.

To do so, the effect of daylength upon the final number of main stem leaves is quantified for wheat varieties of different origin provided their vernalization requirements have been met. Together with the earlier model of leaf appearance, this information is used to calculate the date of flag leaf appearance or that of heading depending on the sowing date. Subsequently the effect of vernalization and temperature on the date of appearance of the last leaf is investigated. This is

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done by comparing observed heading dates of wheat sown at a wide range with calculated dates. The comparison reveals that for a well-defined sowing period vernalization requirements are fulfilled at a very early stage of growth and this can serve as a basis for the model formulation. Finally, the model is validated through comparison of both the predicted final leaf number and the calculated heading date with experimental results from several areas of Europe and the USA.

MODEL DEVELOPMENT

Photoperiodic response of wheat varieties

First, spring wheats, that do not require vernalization, and winter wheats, that are vernalized by presowing treatment, are considered. Such plants are expected to respond immediately after emergence to daylength (Hunt 1979, Rahman 1980).

The relationship between final leaf number and daylength is shown in Fig. 1 for pooled data of 35 spring and vernalized winter varieties, grown in 12 photoperiod-controlled environments. Wheat is a 'long day'

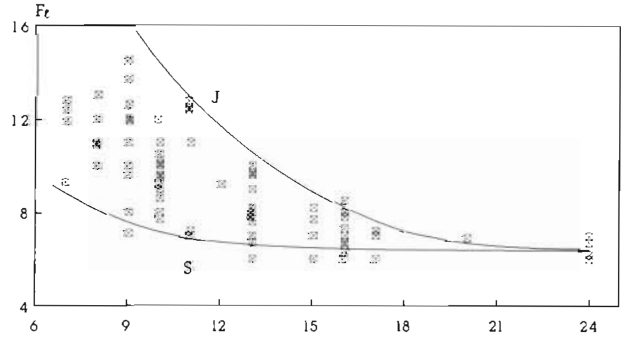


Fig. 1. Final number of leaves (F_1) formed by wheat main stem under different photoperiodic regimes plotted against daylength (d, hours). Lines are fitted curves [see Table 1 and Eq. (1)] of cultivar Justin (J), originating from northern latitudes of Canada, and Sunset (S), that originates much further south. Data from: Halse & Weir (1970), Holmes (1972), Levy & Peterson (1972), Allison & Daynard (1976), Rahman & Wilson (1977), Rahman (1980), Pirasteh & Welsh (1980)

plant, and some varieties are much more responsive to daylength than others. However, when the plants are grown under optimal conditions, the number of leaves is usually 6 or 7 Early investigations with rye suggested that this minimum number of leaves may be necessary before the plant responds to external inductive conditions (Purvis 1934), but later it was also suggested that this is the number of leaves that are already differentiated in the embryo (Holdsworth 1956). Whatever the case, a mean number of 6.5 leaves may be taken as a minimum for all wheat varieties that have been investigated (Fig. 1).

The photoperiodic sensitivity of different varieties can be expressed by the relationship between final number of leaves and daylength. When data from different varieties is kept separate this relationship can be satisfactorily described, for each variety, by the following equation:

$$F_l = \sigma \exp(-\beta\, d) + 6.5 \quad (1)$$

where F_l = final leaf number; d = daylength (h); β = parameter governing the curvature of the relation – it may be set at 0.25 for all varieties; σ = coefficient characterizing the sensitivity to daylength of the variety.

The coefficient σ was estimated by means of a nonlinear fitting method (Ross 1975) and was found to range from 18.39 (σ_{min}) for the variety least sensitive to daylength to 72.52 (σ_{max}) for the most sensitive one. Values of the coefficient σ are given in Table 1 for each of the varieties for which data is given in Fig. 1.

Table 1. Photoperiodic sensitivity (coefficent σ of Eq. [1]) of a number of spring and vernalized winter wheat varieties. Data source is indicated

Cultivar	σ	Source
8–23	50.03	Rahman & Wilson (1977)
8–27	32.31	Rahman & Wilson (1977)
Gabo	30.49	Rahman & Wilson (1977)
Galgalos	65.19	Levy & Peterson (1972)
Justin	72.52	Levy & Peterson (1972)
Kalyansona	32.81	Rahman & Wilson (1977)
Kogat	30.24	Rahman & Wilson (1977)
Marquis	47.74	Holmes (1972)
Natadores	61.95	Levy & Peterson (1972)
Pitic 62	21.50	Levy & Peterson (1972) Holmes (1972)
Selkirk	35.71	Rahman & Wilson (1977)
Siete Cerros	29.53	Allison & Daynard (1976)
Sonora 64	32.83	Allison & Daynard (1976) Pirasteh & Welsh (1980) Levy & Peterson (1972)
Tokwe	18.39	Allison & Daynard (1976)
Triple Dirk	34.52	Rahman & Wilson (1977) Rahman (1980)
Triumph	68.20	Levy & Peterson (1972)
Zambesi 2	32.74	Allison & Daynard (1976)

It can be assumed that sensitivity to daylength is related to latitude of origin. Photoperiodic sensitivity, in fact, can be assumed to be a consequence of the different selection strategies adopted at lower or higher latitudes. At lower latitudes varieties are normally artificially selected for a weak photoperiodic response, in order to promote earliness and escape drought, whereas at higher latitudes varieties are selected for high photoperiodic response to enable a wide range of sowing dates to result in grain-filling during the optimal period around the longest day of the year. The existence of this adaptation of varieties to their photoperiodic environment has often been observed and discussed (Van Dobben 1965, Kirby 1969, Hunt 1979, Hoogendoorn 1985, Krekulè 1987, Napp-Zinn 1987).

If it is assumed that the sensitivity to daylength is correlated to the latitude at which the variety is selected (δ, in degrees), the value of σ can be estimated for varieties whose sensitivity to photoperiod is unknown by means of the following relationship:

$$\sigma = \frac{(\sigma_{max} - \sigma_{min})}{(\delta_{max} - \delta_{min})} = (\delta - \delta_{min}) + \sigma_{min} \qquad (2)$$

where $\delta_{max} = 57°$ latitude; $\delta_{min} = 20°$ latitude.

Model calculations for varieties that do not require vernalization

It is now possible to formulate a model that calculates the final leaf number and the date of flag leaf appearance for any given sowing date and any latitude for wheat plants that respond immediately after emergence to daylength. This is the case in plants that do not require vernalization or are vernalized before emergence.

The model requires the following procedural steps:

(1) Estimation of the time needed from sowing to emergence as a function of temperature. Provided that the soil is moist, this may be done, for instance, by means of the simple relationship between temperature and crop emergence rate reported by Porter et al. 1987 (Appendix 1), or, in more complicated situations, by means of the model developed by Lindstrom et al. (1976).

(2) Determination of daylength at the time of emergence. This may be calculated by the procedure developed by Goudriaan & Van Laar (1978), taking into account the twilight period (Appendix 2).

(3) Calculation of the final leaf number of the variety from the daylength by means of Eq. (1), using the appropriate value of the coefficient σ. The latter value may be determined either in experiments under controlled conditions, or by means of a comparative field trial, or using Eq. (2).

(4) Calculation of initiation and appearance of subsequent leaves from emergence to the moment of appearance of the last leaf. This is achieved using daily mean air temperature and the leaf appearance model presented in the first paper of this series (Miglietta 1990; Appendix 3).

(5) Estimation of heading time just after the appearance of the ligule of the flag leaf.

This procedure was used to calculate the curve relating heading date to sowing date on the basis of the daily mean air temperatures measured in Lelystad (The Netherlands) during the autumn and winter season 1977–78 and for a variety selected at that latitude. This place, period and variety were chosen because they allow comparison with experimental results presented later in this paper.

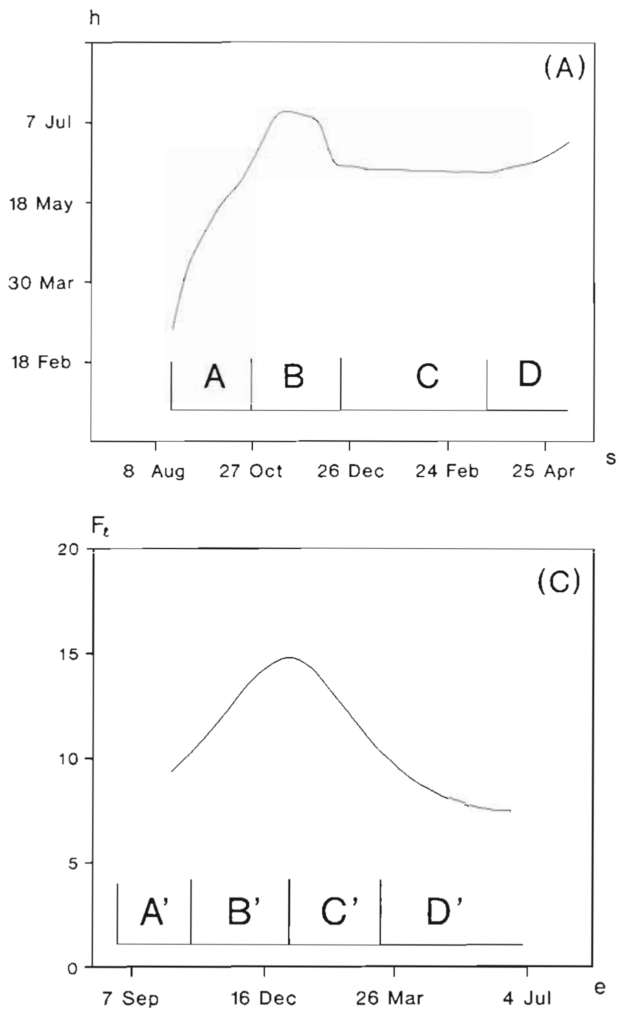
Calculated results are presented in 3 ways: in Fig. 2A, B with the heading date on the vertical axis and the dates of sowing and emergence, respectively, along the horizontal axis, and in Fig. 2C with the final number of leaves on the vertical axis and the date of emergence along the horizontal axis. For subsequent discussion the graph with date of sowing along the horizontal axis is divided into 4 sowing periods, A, B, C and D. The corresponding periods in the graphs with dates of emergence along the horizontal axis are indicated by A', B', C', D'.

For sowing periods before November, in period A, calculated heading dates are very early, in May, because these plants emerge at a time when photoperiod is still so long that the final number of leaves, as calculated by Eq. (1), is low. Plants sown around the middle of November (period B) emerge in the second half of December, when daylength is very short. The final number of leaves is at its highest and heading is postponed to the middle of July. For winter sowing (period C), the heading dates are almost constant because although photoperiod increases and number of leaves decreases when the crops are sown later, plants that are sown earlier do not have any advantage from this due to the low winter temperatures in which leaf appearance stops. This no longer applies for spring sowings (period D) when the synchronization breaks down.

Comparison with a field experiment

A sowing date experiment was carried out by Reinink et al. (1986) in Lelystad in the 1977–78 season using a Dutch winter wheat variety (Lely). Field observations of the heading date are reported in Fig. 3 on the same scales as Fig 2A. The division into periods A, B, and C is also added for easy comparison.

In contrast to the calculated values of Fig. 2A, synchronization was observed to be effective, in the field, from the autumn sowings onwards. This is because for the calculated curve, the seeds of all sowings were assumed to be vernalized, whereas in the actual experiments the autumn sowings were only vernalized in winter when the temperature was sufficiently low. The final leaf number of autumn sowings was, thus, determined by the daylength once vernali-



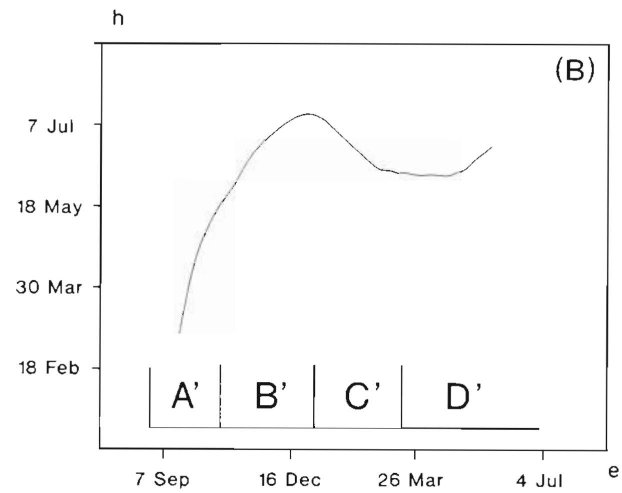


Fig. 2. Development parameters calculated using the procedure described in the text, and on the basis of temperature records measured at Lelystad, The Netherlands, in the season 1977–78. (A) Date of heading (*h*) plotted versus corresponding date of sowing (*s*); (B) date of heading (*h*) versus corresponding date of emergence (*e*); (C) final number of leaves (F_l) versus date of emergence (*e*)

zation requirements were fulfilled and not by the daylength at the time of emergence. Through these vernalization requirements, the plants could escape the early heading dates of period A and the late heading dates of period B. On the other hand, plants sown in the first part of period C were fully vernalized from the beginning by the low winter temperatures, so that their final leaf numbers and heading dates almost coincided with those shown in Fig. 2A. The very small difference between the calculated values and field observations may very well be due to the fact that the daylength sensitivity of the variety used was not determined in the laboratory but had to be estimated from the latitude according to Eqs. (1) and (2). The plants sown in spring, in the last part of period C and in period D, are of course not vernalized, but their synchronization breaks down none the less because, under the higher temperatures, the early sowings remain earlier, throughout their development, than the late sowings.

In temperate climates, vernalization is not a limiting

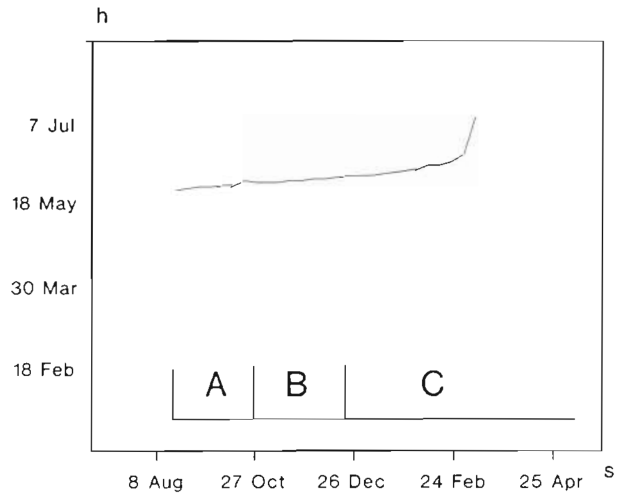


Fig. 3. Heading (*h*) and sowing dates (*s*) observed for winter wheat (cv. Lely) at Lelystad, The Netherlands, in the season 1977–78 (Reinink et al. 1986)

factor for earliness of crops sown at the beginning of period C, i.e. around the coldest period of the year, as was reported by Van Dobben (1947). Hence the final leaf number and the heading date of crop sown at the beginning of the coldest period of the year (within period C) can always be calculated by means of the procedure described earlier for vernalized plants. The final leaf number of earlier sowings (periods A and B) can be calculated assuming that they are more or less synchronized in heading with this late sown crop. For still later sowing (period D) this calculation may break down because of the lack of vernalization in early spring, but this is of no practical consequence because winter wheats are never sown so late.

Imperfect synchronization

Synchronization may be assumed to be perfect, but in practice heading is somewhat later for later sowings as illustrated in Fig. 3. Orsi (1953), O'Leary et al. (1985) and Reinink et al. (1986) found that synchronization is better the colder the climate in winter, and Van Dobben (1947) found that synchronization is poorer for species such as rye that continue to grow at low temperature. This is because the higher the winter temperatures, the more advantage early sowings can gain over late sowings, as was explained above.

If it is assumed that a crop X sown at the beginning of the coldest period of the year is vernalized when it emerges, it can also be assumed that any earlier sowing is fully vernalized at that time. The final leaf number of this early sown crop (F_t) can be calculated to range between a lower value that corresponds to the value of F_l calculated by Eq. (1) for the crop X and an upper value given by F_l plus the number of leaves that are already appeared on its main stem (F_e) when the crop X emerges. Thus F_t is a function of an empirical coefficient μ according to the following equation:

$$F_t = F_l + \mu F_e \quad (3)$$

where F_l = final number of leaves calculated for a crop sown at the beginning of the coldest period of the year, according to Eq. (1); μ = an empirical coefficient ranging from 0 to 1.

The value of the coefficient μ was calculated on the basis of the field experimental data of Reinink et al. (1986) for the seasons 1976–77, 1977–78 and 1978–79. In every season the sowing date closest to the beginning of the coldest period of the year and the corresponding date of crop emergence were identified. Then, for every crop sown earlier the number of leaves that appeared before the emergence of the crop sown at the beginning of the coldest period and the final leaf number were estimated by simulating the leaf appearance (Miglietta 1990; Appendix 3). Finally, values of coefficient μ were estimated by solving Eq. (3).

The results showed a very small variability among sowings and years (0.666 ± 0.033 in 1976–77, 0.637 ± 0.054 in 1977–78 and 0.673 ± 0.054 in 1978–79), although differences in the climatic conditions of the 3 seasons were observed. A mean value of $\mu = 0.65$ seems to be, therefore, appropriate in order to estimate, via Eq. (3), the final leaf number of any crop sown at any date and under any climatic condition, in middle latitudes.

MODEL USE

The model requires the following input:
- Date of sowing
- Date of crop emergence (if known)
- Latitude of the site
- Records of average daily air temperature
- Variety data:
  - Winter or spring wheat
  - Experimentally determined value of coefficient σ or, if this is not available, the latitude at which the variety was selected.

Model output is as follows:
- Date of appearance of subsequent main stem leaves from emergence to heading
- Final number of main stem leaves at heading
- Date of initiation of last leaf at the apex
- Date of heading

The calculation procedure is as follows:

First the 5 procedural steps described above in 'Model development' are executed to estimate the date of emergence and final number of leaves of a crop sown at the beginning of the coldest period of the year (period C). This period is identified, in the model, by means of the 5 d running average of daily air temperature.

Next the appearance of main stem leaves formed by the crop sown at the actual date is simulated over time by means of the model described in the first paper of this series (Miglietta 1991; Appendix 3), and the final number of leaves at the time of emergence for the crop sown at the beginning of the coldest period of the year, is estimated according to Eq. (3).

Finally, heading is assumed to occur immediately after the date of full appearance of the last leaf.

MODEL EVALUATION

To evaluate the model, a large volume of experimental data was collected over a wide range of climatic and photoperiodic conditions. For some experiments, both the final leaf numbers and the dates of heading were measured, but in others only the latter variable was observed. The data concern 58 experimental crops situated in 26 locations throughout Europe and the USA. The experimental locations are shown in Fig. 4 and the data sources are given in Table 2. Observed and calculated values of the date of heading and, where available, of the final leaf number are given in Table 2 and in Figs. 5 & 6. In general, the model performs very well under a wide range of experimental conditions and this provides a good starting point to develop further a more satisfactory onto-morphogenetic model than is available at present.

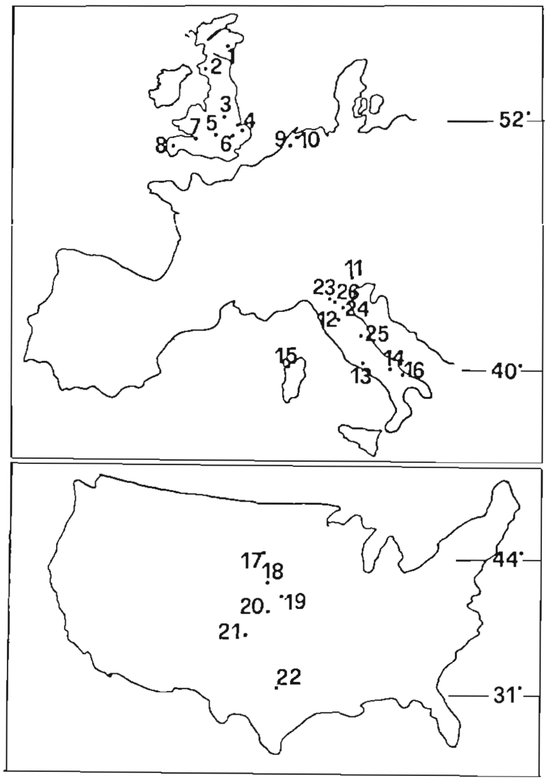


Fig. 4. Western Europe and United States, showing locations of experiments used to validate the model. Site names, countries, latitudes, sowing dates and data sources are listed in Table 2

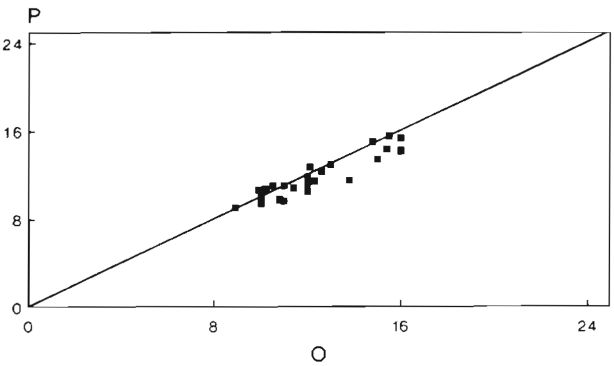


Fig. 5. Scatter diagram of predicted final leaf number (*P*) against corresponding observations (*O*) made in the field experiments listed in Table 2

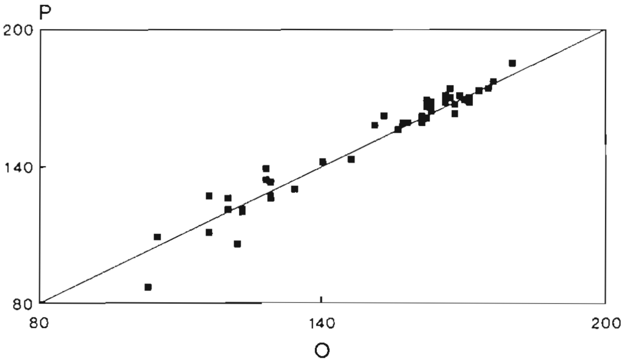


Fig. 6. Scatter diagram of calculated dates of ear emergence (*P*, days from 1 January) against corresponding observations (*O*), made in the field experiments listed in Table 2

DISCUSSION AND CONCLUSIONS

The model clarifies the role of vernalization, photoperiod and temperature within the global development strategy of the wheat plant.

Vernalization increases the range of sowing dates for which the date of heading can be synchronized, by keeping plants insensitive to the still 'long days' of autumn and to the 'short days' of early winter. Photoperiodism determines the final number of leaves on the main stem and contributes, together with the low temperatures, to the synchronization of heading. Thus, a global function seems to be optimized in field crops, that makes the time of flowering occur around the same optimal date for a wide range of sowing dates. The best date for flowering depends on the latitude for which wheat varieties are selected, that is, on their photoperiodic response.

Baker et al. (1980) found a positive correlation between the rate of leaf appearance, expressed in number of leaves per degree days, and the rate of change in daylength at emergence, in experiments where sowing dates varied from autumn to spring. This relation was confirmed by others but only in field experiments, and not under controlled conditions where daylength, temperature and change in daylength were varied independently of each other.

This correlation is confirmed by the model presented here, and can be illustrated by an example using simulation results obtained for Lelystad experiments (Reinink et al. 1986). In the example, the number of main stem leaves appearing over time, calculated by the model for a number of sowing dates ranging from autumn to spring, was plotted against thermal time

Table 2. Final leaf number (F_l) and date of ear emergence (H) calculated for different years, locations and sowing dates are compared with corresponding observed values (F_{lo} and H_o). • Missing values. Numbers correspond to locations in Fig. 4. Data sources are coded as follows: 1 = Porter et al. (1987); 2 = Beni (1984); 3 = Miglietta (1989); 4 = Biancolatte et al. (1982); 5 = Wittmer (1986); 6 = Biancolatte et al. (1983); 7 = Miglietta et al. (1987); 8 = Arkin et al. (1979a, b); 9 = Consorzio Emiliano-Romagnolo Aziende Sperimentali (1977–1986); 10 = Farina et al. (1958); 11 = Capodaglio & Tandoi (1959); 12 = Tandoi (1960–67); 13 = Groot (1986)

No.	Place	Country	Sowing date	F_l	J	F_{lo}	H_o	Source
1	Aberdeen	UK	14 Sep 83	11.4	22 Jun 84	12.3	•	1
	Aberdeen		12 Oct 83	9.9	26 Jun 84	10.0	•	1
	Aberdeen		16 Nov 83	9.0	4 Jul 84	8.9	•	1
2	Auchincruive	UK	14 Sep 83	14.1	18 Jun 84	16.0	•	1
	Auchincruive		12 Oct 83	12.3	20 Jun 84	12.6	•	1
	Auchincruive		16 Nov 83	10.7	22 Jun 84	10.2	•	1
3	Sutton B.	UK	14 Sep 83	14.2	15 Jun 84	16.0	•	1
	Sutton B.		12 Oct 83	11.8	17 Jun 84	12.0	•	1
	Sutton B.		16 Nov 83	10.2	20 Jun 84	10.0	•	1
4	Edmunds	UK	14 Sep 83	14.3	17 Jun 84	15.4	•	1
	Edmunds		12 Oct 83	11.5	19 Jun 84	13.8	•	1
	Edmunds		16 Nov 83	9.7	23 Jun 84	10.8	•	1
5	Cambridge	UK	14 Sep 83	15.0	8 Jun 84	14.8	•	1
	Cambridge		12 Oct 83	12.7	10 Jun 84	12.1	•	1
	Cambridge		16 Nov 83	10.6	12 Jun 84	9.9	•	1
6	Harpenden	UK	14 Sep 83	13.4	17 Jun 84	15.0	•	1
	Harpenden		12 Oct 83	11.2	19 Jun 84	12.0	•	1
	Harpenden		16 Nov 83	10.6	22 Jun 84	10.8	•	1
7	Bristol	UK	14 Sep 83	15.3	11 Jun 84	16.0	•	1
	Bristol		12 Oct 83	12.9	13 Jun 84	13.0	•	1
	Bristol		16 Nov 83	10.8	16 Jun 84	10.5	•	1
8	Newton Abbot	UK	14 Sep 83	15.5	5 Jun 84	15.5	•	1
	Newton Abbot		12 Oct 83	12.9	8 Jun 84	13.0	•	1
	Newton Abbot		16 Nov 83	10.8	10 Jun 84	11.4	•	1
9	Wageningen	Netherlands	21 Oct 82	11.0	8 Jun 83	11.0	10 Jun 83	13
	Wageningen		25 Oct 83	9.6	18 Jun 84	10.0	18 Jun 84	13
10	Nagele	Netherlands	21 Oct 82	10.5	11 Jun 83	11.0	6 Jun 83	13
	Nagele		25 Oct 83	9.4	19 Jun 84	10.0	4 Jun 84	13
11	Lonigo	Italy	28 Oct 83	9.5	20 May 84	•	20 May 84	2
12	Firenze	Italy	21 Nov 86	11.5	11 May 87	12.0	17 May 87	3
	Firenze		21 Nov 86	10.3	29 Apr 87	11.0	4 May 87	3
13	Roma P. G.	Italy	5 Nov 81	14.3	1 May 82	•	4 May 82	4
14	Foggia	Italy	13 Dec 85	9.9	7 May 86	•	9 May 86	5
15	Ottava	Italy	29 Dec 82	9.9	30 Apr 83	•	3 May 83	6
16	Rutigliano	Italy	11 Nov 82	12.8	1 May 83	•	29 Apr 83	7
	Rutigliano		30 Nov 83	11.3	10 May 84	•	14 May 84	7
	Rutigliano		28 Nov 84	10.9	16 Apr 85	•	2 May 85	7
17	Pierre	USA	4 Sep 78	14.3	15 Jun 79	•	11 Jun 79	8
18	Pickstown	USA	8 Sep 78	14.6	12 Jun 79	•	13 Jun 79	8
19	Norfolk	USA	18 Sep 78	13.4	11 Jun 79	•	7 Jun 79	8
20	Grand Isl.	USA	18 Sep 78	13.5	7 Jun 79	•	30 May 79	8
21	Goodland	USA	13 Sep 78	13.3	23 May 79	•	26 May 79	8
22	Blackland	USA	19 Oct 78	14.9	28 Mar 79	•	14 Apr 79	8
23	Mezzano	Italy	12 Nov 76	17.4	2 May 77	•	10 May 77	9
24	Ravenna	Italy	9 Nov 78	12.0	12 May 79	•	21 May 79	9
	Ravenna		15 Nov 79	16.2	16 May 80	•	20 May 80	9
	Ravenna		7 Nov 80	10.7	8 May 81	•	17 May 81	9
	Ravenna		22 Oct 80	12.4	8 May 81	•	16 May 81	9
25	Macerata	Italy	26 Nov 57	11.4	14 May 85	•	8 May 58	10
	Macerata		20 Nov 58	11.1	21 Apr 59	•	26 Apr 59	11
	Macerata		17 Nov 59	11.6	7 May 60	•	26 Apr 60	12
	Macerata		17 Nov 60	11.3	19 Apr 61	•	15 Apr 61	12
	Macerata		21 Nov 61	11.4	19 May 62	•	8 May 62	12
	Macerata		22 Nov 62	10.0	13 May 63	•	9 May 63	12
	Macerata		15 Nov 63	10.4	6 May 64	•	30 Apr 64	12
	Macerata		20 Nov 64	10.7	13 May 65	•	8 May 65	12
	Macerata		15 Nov 66	10.4	3 May 67	•	27 Apr 67	12
26	Boara	Italy	10 Nov 80	9.3	5 May 81	•	16 May 81	9

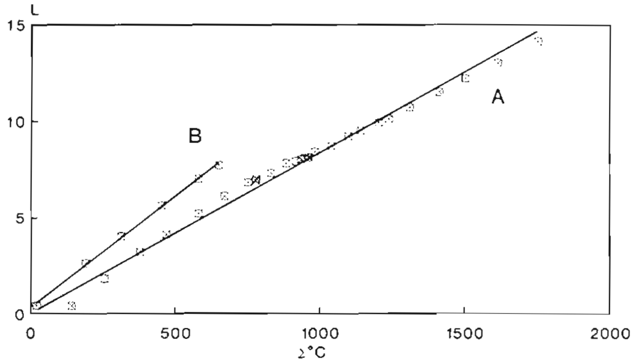


Fig. 7. Simulated number of appeared main stem leaves (L) plotted versus thermal time calculated from emergence (Σ °C), for 2 of the 50 sowings made in the field experiment reported by Reinink et al. (1986). A: sown on 31 August 1978; B: sown on 29 May 1979

(base temperature 0 °C) calculated, for each sowing date, from emergence of the appearance of last leaf (Fig. 7). Subsequently, the slopes of the lines fitted on the data, corresponding to the rates of leaf appearance per degree days, were related to the rate of change in daylength calculated at the time of emergence of each sowing. The slope of this relation appears to be very close to that found experimentally, both in direction and magnitude (Fig. 8).

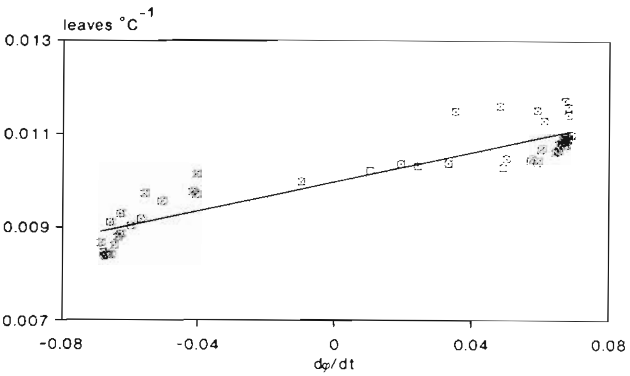


Fig. 8. Rates of leaf appearance calculated by the regression of the simulated number of appeared leaves on thermal time (leaves $°C^{-1}$) plotted against rate of change in daylength at crop emergence ($d\varphi/dt$). Line represents the linear relationship found by Baker et al. (1980)

The divergence of the 2 lines of Fig. 7 is due both to the different base temperature assumed in the model and in the computation of thermal time, and to the fact that the period from initiation to appearance of a leaf increases with increasing leaf number as quantified in the first paper of this series (Miglietta 1990). This makes the average rate of appearance of any given crop lower, the greater the final number of leaves. Since the final number of leaves is lower in spring when the days lengthen and the temperature is higher than in autumn when the days shorten and the air temperature is lower, there has to be a correlation between the rate of leaf appearance and the rate of change in daylength. This correlation, significant as it is, does not however reflect a causal relation.

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APPENDIX 1

In the model, daily rates of crop emergence (Er) are calculated as a linear function of the mean daily air temperature (T) according to the following equation:

$$Er = -0.006 + 0.0065\ T \qquad \text{for } T > 0.92\ °C$$

A crop emergence stage (Es) is then calculated as the sum of the daily values of Er. Crop emergence is finally assumed to occur when Es is equal or greater than 1.

APPENDIX 2

When the date of crop emergence is known (D = number of days since January), the sun declination (θ) is calculated as follows:

$$\theta = -23.45 \cos[360(D+10)/365]$$

Then the photoperiodic daylength (d, including the twilight zone) is calculated as a function of sun declination (θ) and latitude (δ):

$$d = 12\left[1 + 2\arcsin\left([-\sin(-4)+\sin\theta\sin\delta]/\cos\theta\cos\delta\right)/180\right]$$

APPENDIX 3

The daily rate of leaf primordia initiation at the wheat apex (Pr) is calculated as a linear function of the daily mean air temperature (T) according to the following equation:

$$Pr = -0.038 + 0.0149\ T \qquad \text{for } T > 2.55\ °C$$

The total number of initiated leaf primordia (P) is then computed as the sum of daily rates of initiation assuming that the number of primordia that are already initiated at the time of crop emergence is fixed ($P_0 = 4$). The number of leaves that have appeared on the main stem (L) at any given time of the growing cycle is finally computed as a function of the number of initiated primordia according to the following equation:

$$L = \frac{1 - \exp(-0.03\,(P - P_o))}{0.03}$$

The simulation stops when the value of L is equal or greater than the predicted final leaf number (F_l).

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