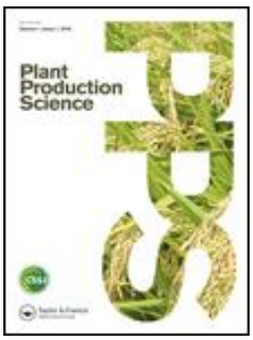


Plant Production Science

ISSN: (Print) (Online) Journal homepage: https://www.tandfonline.com/loi/tpps20

Morphological and phenological adaptation for convergent development of tillers in Widely spaced wheat sown on different dates

Masanori Toyota & Masahiro Morokuma

To cite this article: Masanori Toyota & Masahiro Morokuma (2020): Morphological and phenological adaptation for convergent development of tillers in Widely spaced wheat sown on different dates, Plant Production Science, DOI: 10.1080/1343943X.2020.1808485

To link to this article: https://doi.org/10.1080/1343943X.2020.1808485

Published online: 31 Aug 2020.

PLANT PRODUCTION SCIENCE
https://doi.org/10.1080/1343943X.2020.1808485

REGULAR PAPER

OPEN ACCESS Check for updates

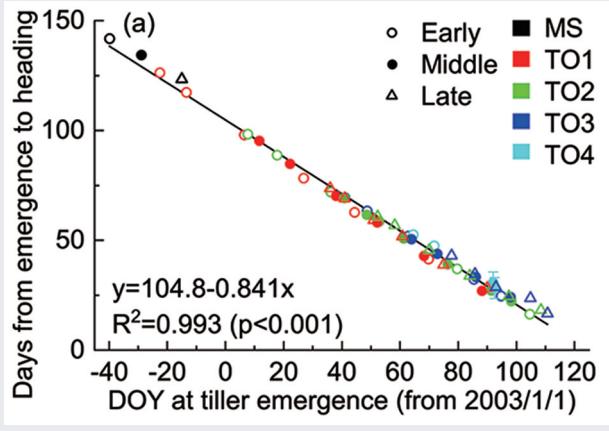
Morphological and phenological adaptation for convergent development of tillers in Widely spaced wheat sown on different dates

Masanori Toyota and Masahiro Morokuma

Faculty of Agriculture, Kagawa University, Kagawa, Japan

ABSTRACT

This study analyzes the dynamics of leaf and tiller emergence and development of widely spaced wheat sown on different dates. We used the phyllochron (time interval between the emergence of successive leaves at the same stage), site filling (the relative rate of increase in the number of tillers per phyllochron), and indices associated with 'the synchronous growth'. Number of productive tillers per plant (including the main shoot, MS) reached 45.7 in early sowing, and significantly decreased by the delay in sowing. The increase in tiller number with the elapse of leaf age (Haun stage) of MS (HS_{ms}) was almost the same as that expected from synchronous growth until HS_{ms} 8.6 and site filling before this HS_{ms} was close to 0.481. The phyllochron was shortest in MS and increased in axillary tillers with increasing tiller order and position, but the differences in phyllochron between MS and axillary tillers within a plant were significant only at higher order and positions of tillers. The time of emergence of tillers was always advanced in comparison with that expected from synchronous growth. A very close negative linear relationship was found between the number of days from emergence to heading of tillers and the time of their emergence expressed as day of year; this relationship was independent of the tiller order, position and sowing date. Although the phyllochron gradually became longer, a progressive decrease of the leaf and spikelet per spike with the increasing tiller order and position may contribute considerably to the convergence to heading time.



ARTICLE HISTORY
Received 20 January 2020
Revised 2 June 2020
Accepted 28 July 2020

KEYWORDS
Triticum aestivum; wheat; phyllochron; tillering; site filling; sowing date

Introduction

Dry matter production of Poaceae crops is largely determined by the size of the leaf area, which is regulated by the kinetics of emergence, growth, and senescence of tillers and leaves. Detailed quantitative description of tiller and leaf dynamics may contribute to increasing crop yield potential and to improving the accuracy of crop simulation models. The development of Poaceae crops has been quantified based on the concept of building canopies by the formation, growth and senescence of phytomers, which is the unit comprised of the leaf, axillary bud, node, and internode (McMaster, 2005). Based on the phytomer concept, leaf and tiller number dynamics in wheat are frequently quantified by the phyllochron (time interval between the emergence of successive leaves at the same stage; Wilhelm & McMaster, 1995) and site filling (the relative rate of increase in the number of tillers per phyllochron; Bos & Neuteboom, 1998; Davies, 1974; Neuteboom & Lantinga, 1989).

CONTACT Masahiro Morokuma morokuma.masahiro@kagawa-u.ac.jp

The phyllochron and its reciprocal, the leaf appearance rate (LAR) are used to analyze the genetic and environmental effects on plant development (Alzueta et al., 2012; Ochagavía et al., 2017) and in growth simulation models (Abichou et al., 2018; Baumont et al., 2019; Evers et al., 2007). The phyllochron is affected by sowing date (Kirby et al., 1985; Miralles et al., 2001; Mulholland et al., 1997), temperature, day length (Cao & Moss, 1994), and N status of soil (Longnecker et al., 1993). Site filling, or tillering is controlled by genetical and environmental factors. Tiller number dynamics is the result from the number of tillers that grow to tillers among the total number of tiller buds, so that the outgrowth of tillers largely depends on the availability of resources such as nutrients (Dreccer et al., 2013) and light intensity (Bos & Neuteboom, 1998). In addition, light quality (red/far-red ratio, R:FR) is closely related to tiller production and abortion (Ballaré & Casal, 2000; Evers et al., 2006; Sparkes et al., 2006; Toyota et al., 2014).

Because tillering ceased earlier at higher population densities in wheat (Evers et al., 2006), the lower the planting density, the higher the number of tillers emerge from a plant. Katayama (1951) devised 'the concept of uniform cohorts' which illustrates the regularity of leaf and tiller dynamics of isolated rice and wheat that has many emerged tillers. Goto and Hoshikawa (1988) defined as 'the synchronous growth' on the basis of a putative growth pattern derived from Katayama's concept. The synchronous growth assumes that the potential number of tillers per phyllochron follows the Fibonacci series (one tiller increase $e^{0.481}$ times per one phyllochron). In reality, however, the increase of leaf and tiller number in rice not always match with that expected from synchronous growth (Goto & Hoshikawa, 1988).

In the present study, we investigated the morphology and development of leaf and tiller in widely spaced wheat sown on three different dates to expand the number and variation of tillers. The result showed that the number of tiller emergence per phyllochron was almost the same as that expected from synchronous growth until a certain leaf age (Table 3). This result raises the question of whether the emergence of individual tillers coincides with the timing expected from synchronous growth, or varies by the tiller positions. And if it varies by its position, the regularity that enables the number of tiller emergence follows the Fibonacci series should be elucidated.

On the other hand, the mechanisms of convergent development of wheat with a wide range of sowing dates are not fully understood. For example, the time of flowering in winter wheat sown with a wide range of sowing dates from September to March (181 days) in southwestern Scotland narrowed to only 16–20 days from June to July (Hay, 1986). In Australia, a 113-day difference in sowing dates from May to July narrowed to 38–47 days in spring and winter type wheat, respectively (Manupeerapan & Pearson, 1993). Thus, cereal crops are able to converge on the most favorable period (Hay & Kirby, 1991), but the underlying mechanisms remain unclear.

In the present study, we found a very close negative linear relationship between the number of days from emergence to heading of tillers and the time of their emergence expressed as day of year regardless of the tiller order, position and sowing date (Figure 5(a)). The convergence of development within and between plants shown in Figure 5(a) should be accompanied by a progressive shortening of the phyllochron (acceleration of leaf appearance rate) or a decrease in the number of organs such as final leaf number and the number of spikelets per spike. Our second question is what morphological and phenological regulation exists that enables convergent development of heading time.

This study investigates the dynamics of leaf and tiller emergence and development of widely spaced wheat sown on three different dates. The objectives were to: (1) explore whether the emergence of individual tillers coincides with the timing expected from synchronous growth and if not, what regularity enables the number of tiller emergence to follow the Fibonacci series, and (2) elucidate the mechanisms that underlie the linear relationship between the number of days from emergence to heading of tillers and the time of their emergence expressed as day of year. For these purposes, we analyze the dynamics of leaf and tiller emergence and development using the phyllochron, site filling, and indices associated with 'the synchronous growth'.

Materials and methods

Study site, plant material and treatments

A field experiment was conducted under natural climatic conditions in the experimental field of Kagawa University, Japan (E 134°7′, N 34°16′) during the 2002–2003 growing season. Spring wheat (*Triticum aestivum* L., 'Sanukinoyume 2000') were sown manually at a 2 cm depth with wide spaces (0.7 m × 0.8 m) on November 5 (early), November 19 (middle), and December 3 (late) in three replicated plots (1.4 m × 1.6 m) containing four plants each. Compound fertilizer (N, 0.10 g g^{-1}; P_2O_5, 0.08 g g^{-1}; K_2O, 0.10 g g^{-1}) was applied twice at the seedling emergence and spike formation stages, at a rate of 5.4 g m^{-2} of N.

Air temperature, daily total solar radiation, and daily precipitation were measured at the meteorological

station of the Faculty of Agriculture, Kagawa University, which is located adjacent to the experimental field. The 15-year mean values from 2001 to 2015 at the meteorological station were compared with the values in 2002–2003 season.

Plant measurement

We measured 6 well growing plants (2 plants from each of the 3 replicated plots) selected from 12 plants (4 plants per plots) for each sowing date. The leaf blade length of the youngest and second youngest visible leaves for all visible tillers including the main shoot (MS) was recorded nondestructively twice a week. If the ligule of the youngest leaf had not appeared from the leaf sheath of its parent tiller, only the blade length of the youngest leaves was recorded. Leaf positions and the name of the tiller or MS were recorded using the naming system developed by Klepper et al. (1982, 1983). The combination of 'L' (leaf) or 'T' (tiller) and '#' (acropetal order of organ within a plant) identifies a specific leaf or tiller as 'L#', 'T#' or 'T##'. For example, 'L1' is the first foliar leaf of MS, 'T1' is the primary tiller derived from the axil of L1 in MS, and 'T10' is the secondary tiller emerged from the prophyll of T1. The leaves on tillers are expressed as L#.#; for example, L1.1 is the first leaf of T1, and L10.0 is the prophyll of T10. Tiller order (TO) is expressed as TO1, TO2, and TO3 for the primary, secondary and tertiary tiller, respectively. Coleoptile tiller (T0) were not included in this study because the rhizome separetes morphologically between T0 and T1 or higher tillers (Percival, 1921), and T0 is more susceptible than other tillers to environmental conditions (Peterson et al., 1982; Rawson, 1971). In the present study, though T0 did not emerge in most plant, we thinned emerged T0 at the early vegetative stage. The final leaf number (FLN), the time of heading, and number of spikelets per spike for MS and productive tillers were recorded.

Haun stage (HS; Haun, 1975) is a numerical expression widely used to quantify the stages of Poaceae development. HS for MS (HS_{ms}) and any axillary tiller (HS_t) were used to quantify the development of each tiller. HS was calculated as (Haun, 1975; McMaster, 2005):

$$HS_{ms\ or\ t} = (n-1)\ + \mathrm{Ln}/\mathrm{Ln} - 1 \quad (1)$$

where n is the number of visible leaves on the tiller, L_{n-1} is the blade length of the second youngest leaf on the tiller, and L_n is the blade length of the youngest leaf extending from the enclosing leaf sheath. The data used were recorded from the appearance of the first leaf ligule until the appearance of the last leaf (i.e. flag leaf) ligule of the tillers.

The elapse of plant and shoot development was expressed as a calendar day or growing degree-days, the cumulative temperature above the base temperature (GDD, °Cd). GDD was calculated using the following equation:

$$\mathrm{GDD} = \sum[(T_{max} + T_{min})/2 - T_b] \quad (2)$$

where T_{max} and T_{min} are daily maximum and minimum temperature, respectively, measured at 1.5 m above the soil surface, and T_b is the base temperature assumed to be 0°C (Baker et al., 1980; Kirby et al., 1985).

Terminology of the synchronous growth

On the basis of the phytomer concept (McMaster, 2005), we used indices associated with 'the concept of uniform cohorts' (Hanada, 1993; Katayama, 1951). Goto and Hoshikawa (1988) defined 'the synchronous growth' (putative growth pattern derived from Katayama's concept) as follows: (1) the appearance of leaf N on a tiller is synchronized with that of the first leaf on the tiller, which is formed on the axil of leaf (N – 3), and (2) every tiller in the same plant has the same phyllochron interval. The definitions mean that two phyllochrons separate the emergence of a tiller and its first daughter tiller; the potential number of tillers per phyllochron follows the Fibonacci series (Bos & Neuteboom, 1998; Skinner & Nelson, 1992).

Goto and Hoshikawa (1988) also devised the relative tiller position (RTP), which indicates the acropetal tiller position arranged by the theoretical order of tiller emergence expected from synchronous growth:

$$\mathrm{RTP} = \mathrm{n1}\ + \mathrm{n2}\ + \mathrm{n3}\ + \mathrm{n4}\ \ldots \mathrm{ni} + 2\mathrm{N} = \Sigma ni + 2\mathrm{N} \quad (3)$$

where ni is the number of each digit from left to right of the tiller name, and N is the number of digit. For example, RTP of T1 is 3 (1 + 2), T10 is 5 (1 + 0 + 4), and T210 is 9 (2 + 1 + 0 + 6). Illustration of the calculation of RTP is shown in Figure 1. Synchronous growth assumes that tillers with the same RTP emerge simultaneously and grow at the same rate (same phyllochron intervals).

The relative tiller age (RA) is the sum of RTP and HS_t of axillary tillers (Goto & Hoshikawa, 1988); this index enables an easy comparison of the progress of tiller age within the same RTP group. For example, RA for T1 (RTP 3) at HS_t 1.1 is 4.1 (RA = RTP+HS_t = 3 + 1.1 = 4.1).

Analysis of leaf and tiller dynamics

We defined the time of individual tiller emergence as the day when we first recognized the appearance of

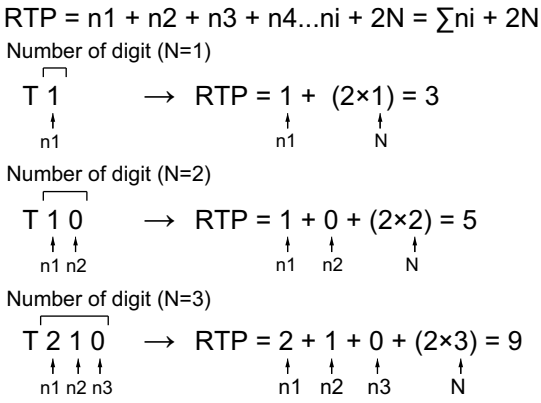


Figure 1. Illustration of the calculation of relative tiller position (RTP).

a new leaf tip of the tiller above the leaf sheath of its parent tiller. To calculate LAR [leaf (°Cd)$^{-1}$] and its reciprocal, the phyllochron [(°Cd) leaf $^{-1}$] for every shoot, a simple linear regression between HS and GDD was used. The data of the tillers were excluded from the analysis if the significance level of a linear regression was higher than 0.05. If the data were available for three or fewer of six plants, they were excluded from the calculation of the mean value of each tiller for a particular sowing date.

The relationships between tiller number per plant and elapsed HS_{ms} were calculated from the plant measurements, but this was inconvenient because the HS_{ms} of plants measured was mostly limited to 10, when tiller emergence had not yet ceased. Therefore, a simple linear regression between HS_{ms} and GDD was applied to convert the relationship between tiller number per plant and GDD to that between tiller number per plant and elapsed pseudo HS_{ms}, which assumes that new leaves appear with same phyllochron intervals even after the full appearance of the flag leaf of MS.

The number of tillers per plant plotted against pseudo HS_{ms} until the maximum number of tillers followed a sigmoidal curve, so that the Richards function (Richards, 1959) was applied to the relationship:

$$\text{no. tillers plant}^{-1} = A\left[1 + e^{(b - k\text{HS}_{ms})}\right]^{-1/n} \quad (4)$$

where A is the asymptotic maximum number of tillers per plant, e is the base of the natural logarithm, and n, b, and k are model parameters.

Wheat tillering dynamics can be quantified with the phyllochron and site filling, the relative rate of the increase in the number of tillers per phyllochron (Bos & Neuteboom, 1998; Davies, 1974; Neuteboom & Lantinga, 1989). Site filling (Fs) is generally calculated as:

$$\text{Fs} = (\ln T_1 - \ln T_2)/(t_2 - t_1) \quad (5)$$

where T_1 and T_2 are tiller numbers (including MS) at the time t_1 and t_2, expressed as HS_{ms}. In this study, site filling was calculated graphically from the relationship between tiller number expressed on a natural log scale and HS_{ms} (Gautier et al., 1999). Because two lines appeared to be jointed at a point, a piecewise regression model (Toms & Lesperance, 2003) was fitted:

$$\ln(\text{no. tillers plant}^{-1}) = \begin{cases} b + Fs_1 x, \ if\ x \le a \\ b + Fs_1 a + Fs_2(x - a), if\ x > a \end{cases} \quad (6)$$

where x is pseudo HS_{ms}, b is the intercept of the model, and Fs_1 and Fs_2 are the slopes of the lines corresponding to site filling before and after the breakpoint (a), respectively.

The index to evaluate the synchrony of tiller emergence is HS-delay (the difference between the HS of a tiller and the HS of its parent tiller above the leaf from which the axil tiller emerges; Bos & Neuteboom, 1998) (Figure 2). HS-delay evaluates the synchrony between a tiller and its parent tiller. The HS_{ms}-RA index evaluate the synchrony of emergence of a tiller and its theoretical time of emergence in HS_{ms} assumed from synchronous growth. The timing of the calculation of HS-delay and HSms-RA was at the first measurement of leaf blade length after the appearance of the leaf ligule of the first leaf of the tiller. Synchronous growth assumes that tiller number increases with elapsed HS_{ms} according to the Fibonacci series, and in this case HS-delay becomes 2 (Bos & Neuteboom, 1998) and HS_{ms}-RA becomes 0. For example, HS-delay of T1 (1.45) in Figure 2 means that HS_t of T1 is advanced 0.55 compared with the HS_t expected from synchronous growth. For another example, if the HS_t of T11 is 1.6 at HS_{ms} 7.1, this means that HS_t of T11 is advanced 0.5 compared with the HS_t expected from synchronous growth. Because the RA of T11 at HS_t 1.1 is 7.6 (RA = RTP+HS_t = 6 + 1.6 = 7.6), therefore HS_{ms}-RA is −0.5 (i.e. 7.1 − 7.6 = −0.5).

Statistical analysis

Differences in morphological characteristics, phenological stage and duration, phyllochron, site filling, breakpoint, HS-delay and HS_{ms}-RA among sowing dates were determined using ANOVA. When ANOVA detected a significant difference, the means were compared using the Tukey's HSD test. Differences were considered significant at $p < 0.05$. All statistical tests, linear regression and non-linear model fitting

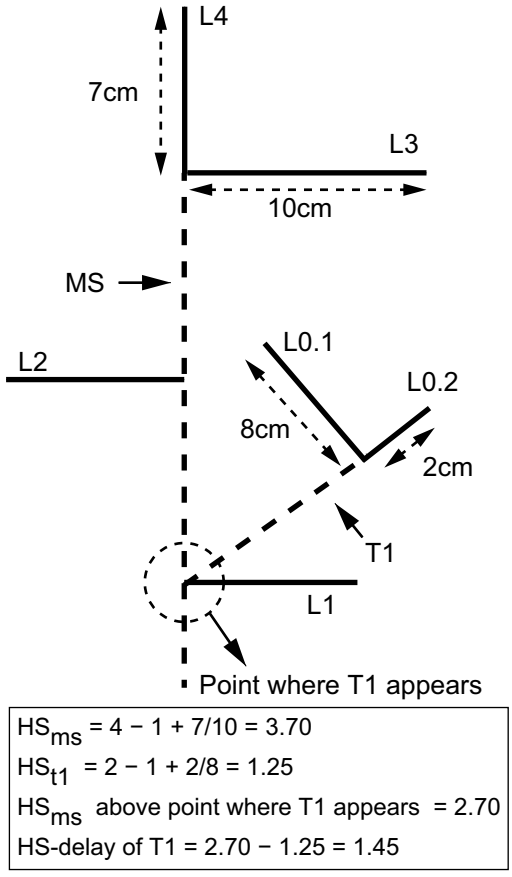


Figure 2. Illustration of the calculation Haun Stage in main stem (HS_{ms}) and tiller (HS_t) and HS-delay. Leaf sheaths are indicated by dashed lines, leaf blades by solid lines and the lengths of the two youngest leaf blades per tiller are given (cited from Figure 2 in Bos & Neuteboom, 1998).

were performed in JMP 13 statistical software (SAS Institute Japan, Tokyo, Japan).

Results

Meteorological condition

Figure 3 shows the changes in mean temperature, daily total solar radiation, and precipitation at 10-day intervals during the 2002–2003 experimental periods. Hereafter, all significant differences in Figure 3 are based on the comparison with the 95% confidence interval of the 15-year means (2001–2015). The mean temperature in November was significantly lower than the 15-year means, but there was no particular trend in mean temperature after December. Solar radiation in 2002–2003 season was significantly higher than the 15-year means for many periods. There was no rainfall in mid-November. Precipitation was significantly lower in late March and mid-April.

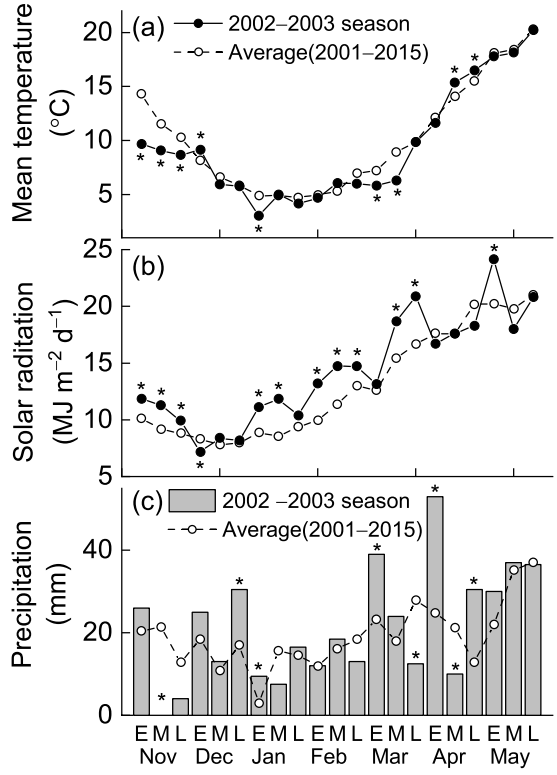


Figure 3. Changes in (a) mean temperature, (b) daily total solar radiation, and (c) precipitation at 10-day intervals (i.e. an average of three times per month) to represent the early (E), middle (M), and late (L) parts of the month during the experimental periods in 2002–2003. Averages represent the mean from 2001 to 2015. Asterisks (*) indicate values outside of the 95% confidence interval for the 15-year mean (i.e. significantly higher or lower values).

The number of tiller, final leaf number, and duration from sowing to heading in MS

The number of tillers per plant and the duration from sowing to heading of MS (in days and accumulated GDD) were significantly decreased by delay in sowing, whereas the final leaf number on MS was not affected by sowing date (Table1). We attributed the decrease in the number of tillers to a decline in the percentage of

Table 1. Number of tillers per plant, final leaf number (FLN) on the main stem (MS), and duration (number of days and accumulated GDD) from sowing to heading in wheat sown on different dates.

Sowing	Number of tillers per plant	FLN on MS	Duration	
			Days	GDD (°Cd)
Early	45.7 a†	10.2	159 a	1122 a
Middle	38.2 b	10.2	148 b	1043 b
Late	35.5 b	10.2	137 c	962 c

†Means (n = 6) followed by the different letter within a column are significantly different between sowing date by Tukey's HSD ($p < 0.05$).

tiller emergence at RTP 8 and above, whereas the percentage of emergence was not affected by sowing date below RTP 8 (Figure 4).

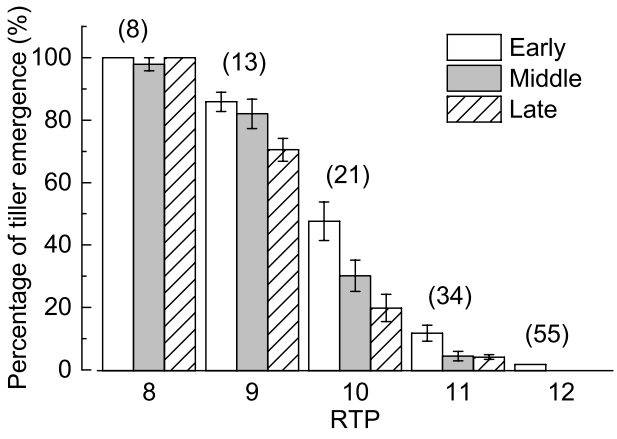


Figure 4. The percentage of emerged tillers relative to the potential number of tillers according to the synchronous growth theory. Values are the means and the error bars show standard error of the mean (n = 6). Numbers above bars are potential numbers of tillers for each relative tiller position (RTP). The percentages at RTP < 8 were 100%.

Duration of tillering and heading and from emergence to heading

The duration of tillering (without MS) within a plant decreased significantly with the delay in sowing, whereas the duration of heading (including MS) was not differed (Table 2). The longest and shortest duration from emergence to heading of tillers was significantly decreased by the delay in sowing (Table 2). The difference in the duration of tillering within a plant (78–126 days) converged to a 19–24 days difference in the duration of heading. The longest duration from emergence to heading in tillers (123–142 days in MS) was shortened to 14–18 days for the tillers that had the shortest duration from emergence to heading (Table 2).

The number of days from emergence to heading of tillers was significantly associated with the day of year (DOY, from 2003/1/1) of tiller emergence regardless of the sowing date and tiller order (Figure 5(a)). On the other hand, the relationship between days from emergence to heading and the time of emergence in GDD,

Table 2. Duration of tillering (without MS) and heading (including MS) within a plant and the longest and shortest duration from emergence to heading of tillers (including MS) in wheat sown on different dates.

	Duration of tillering within a plant/ (without MS)		Duration of heading within a plant/ (including MS)		Duration from emergence to heading of tillers/(include MS)			
					Longest		Shortest	
Sowing	Days	GDD (°Cd)	Days	GDD (°Cd)	Days	GDD (°Cd)	Days	GDD (°Cd)
Early	125.8 a[†]	830.2 a	24.3	407.7	141.8 a	832.4 a	17.2 a	273.6
Middle	90.5 b	639.0 b	19.3	331.6	134.5 b	714.4 b	18.0 b	292.2
Late	77.7 c	721.4 b	22.0	384.3	123.3 c	655.4 ab	14.3 ab	240.0

[†]Means (n = 6) followed by the different letter within a column are significantly different between sowing date by Tukey's HSD (p < 0.05).

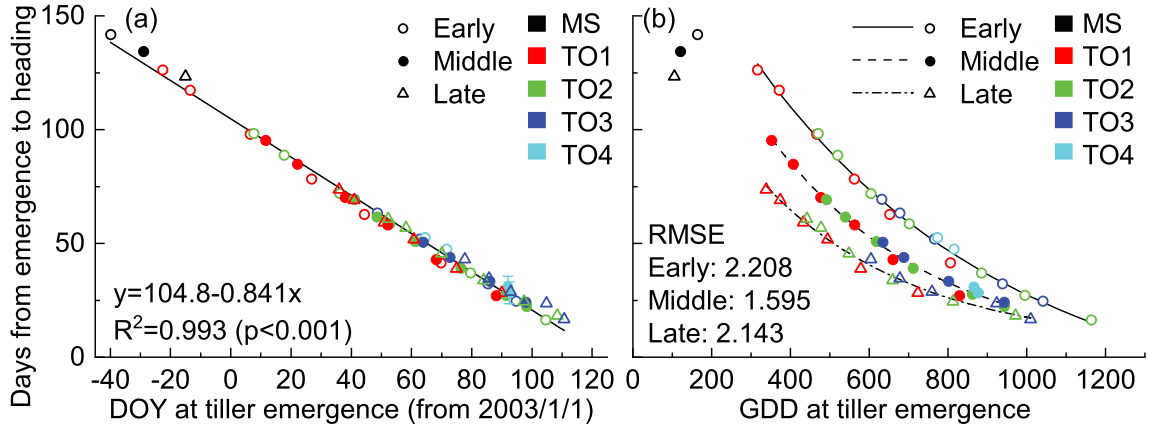


Figure 5. Relationship between days from emergence to heading and (a) day of year (DOY) at tiller emergence and (b) GDD at tiller emergence. In (a), the strait line represents linear regression for the pooled data of all tillers and sowing dates; the coefficient of determination (R^2) and the level of significance (p) are shown. In (b), the curve represents nonlinear model fitting for each sowing date; the data for main shoots were excluded. Early: Days = $169.748 \times e^{(-0.00261 \times GDD) + 5.164}$, middle: Days = $224.172 \times e^{(-0.00242 \times GDD) + 0.5083}$, late: Days = $253.766 \times e^{(-0.00155 \times GDD) - 26.539}$. TO, tiller order; RMSE, root mean square error.

except for the MS, was well fitted by an exponential decay model for each sowing date (Figure 5(b)). The days from emergence to heading shortened exponentially with the delay in tiller emergence in GDD. The difference in days from emergence to heading was largest at around 300 °Cd and gradually converged as GDD increased.

Tiller number dynamics and site filling

he linear relationship between HS_{ms} and GDD was highly significant regardless of the sowing date (Figure 6). The mean leaf appearance rate of MS increased significantly with delay in sowing (data not shown). Tiller number showed a sigmoidal increase with elapsed pseudo HS_{ms}

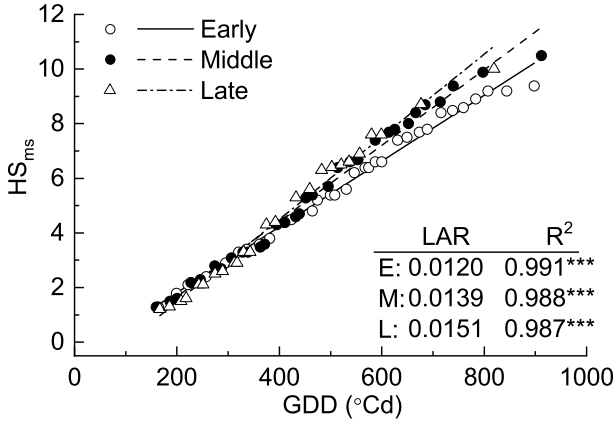


Figure 6. Relationships between HS_{ms} and GDD for wheat. Lines represent linear regression for each sowing date. Data and fitted lines are shown for a representative plant for each sowing date. Leaf appearance rate [(LAR, leaf °Cd^{-1})] and coefficient of determination (R^2) are also shown. *** $p < 0.001$.

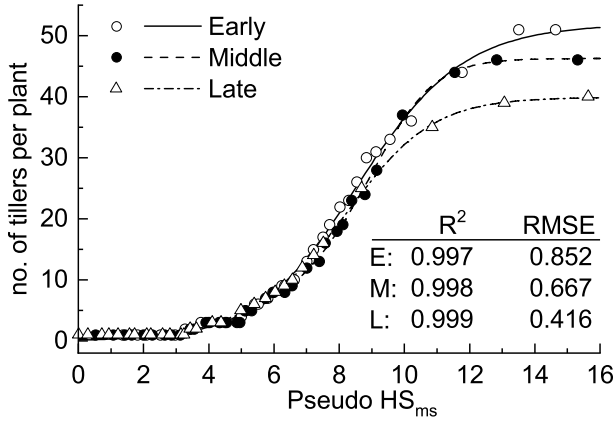


Figure 7. Relationships between the number of tillers per plant and pseudo HS_{ms}. Curves represent nonlinear model fitting (Richards model [4]) performed for each sowing date. The coefficient of determination (R^2) and root mean square errors (RMSE) of the model are shown. Data and fitted lines are shown for a representative plant for each sowing date.

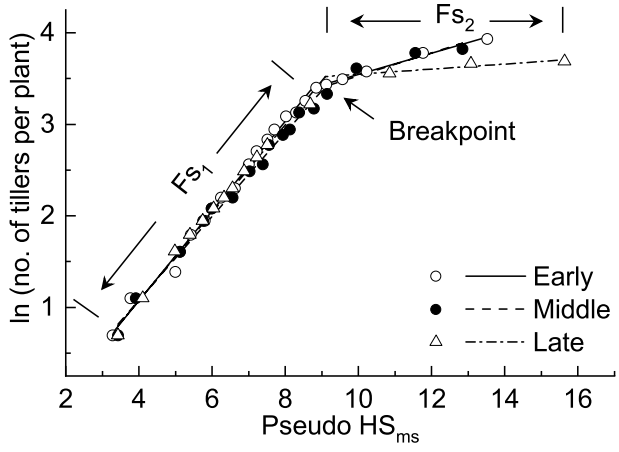


Figure 8. Relationships between the natural log of the number of tillers per plant (including the main shoot) and pseudo HS_{ms}. Broken-stick lines represent nonlinear model fitting (piecewise regression model [6]). Data and fitted lines are shown for a representative plant for each sowing date.

of a representative plant for each sowing date (Figure 7). No clear differences among sowing dates were observed until pseudo HS_{ms} 8, but then after the increase in tiller number was slower with later sowing dates.

The same relationships are shown in Figure 8, except that tiller number per plant is expressed on the natural log scale. For all plants, two lines were jointed at a point, resulting in 'broken-stick' shape. Thus, site fillings before and after the breakpoint was estimated by fitting a piecewise regression model [6]. The sowing date did not affect the Fs_1 and the breakpoint, but the Fs_2 of late sowing was significantly lower than that of middle sowing (Table 3, Figure 8). The Fs_1 of every sowing date was very closed to the theoretical value (0.481) of the Fibonacci series assumed from synchronous growth.

Phyllochron and the timing of tiller emergence

The phyllochron of the tillers estimated by the linear regression model between HS_t and GDD for every emerged tillers decreased significantly with the delay in sowing except in TO1 (RTP5 and RTP7) and TO3 (Figure 9). A significant difference in phyllochron among tillers

Table 3. Site filling before and after the breakpoint estimated by a piecewise regression model, breakpoint (HS_{ms}), and the intercept of the model.

Sowing	Fs_1†	Fs_2†	Break-point (HS_{ms})	Intercept
Early	0.481	0.107 ab‡	8.80	−0.830
Middle	0.480	0.146 a	8.39	−0.836
Late	0.479	0.050 b	8.81	−0.894

†Site filling before (Fs_1) and after (Fs_2) the breakpoint.
‡Means (n = 6) followed by the different letter within a column are significantly different between sowing date by Tukey's HSD ($p < 0.05$).

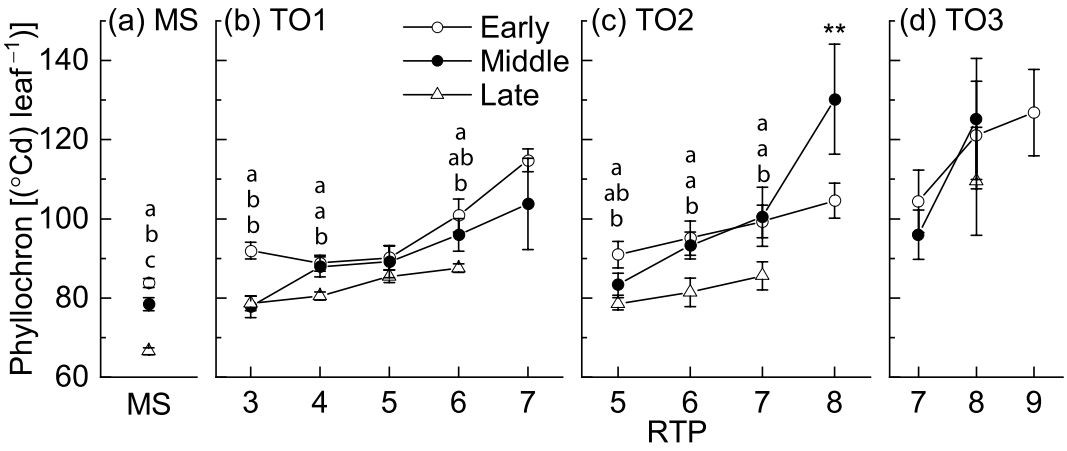


Figure 9. Phyllochron of tillers estimated by a simple linear regression model between the Haun stage of the tiller (HS_t) and GDD for every individual tiller. Phyllochrons were classified by the tiller order (TO) and relative tiller position (RTP). Data points are means and error bars represent standard error of the mean. Number of data points for the mean varied according to the order and position of tillers. Different letters above the symbols indicate significant differences among sowing dates by Tukey's HSD ($p < 0.05$). Letter order corresponds to the vertical position of the symbols within the same RTP. ** in (c) indicates significant difference between sowing dates by *t*-test ($p < 0.01$).

within a plant was observed in early and middle sowing but not in late sowing (Table 4). The phyllochron of MS is the shortest or second shortest among tillers within a plant and it gradually became longer with increasing the order and position of tillers in early and middle sowing (Table 4, Figure 9).

The HS-delay was significantly larger in late sowing than in early and middle sowing in TO1(RTP 3 – 5 and RTP 7) and TO2 (RTP 6 and RTP 7), indicating that the time of tiller emergence from its parent tiller in late sowing tended to be later than in early and middle sowing (Figure 10). However, the HS-delay were below 2 in all tillers except RTP 3 in TO1 (2.03) and RTP 8 in TO3(2.01) in late sowing, and it was the lowest at RTP 5 in TO1 in early sowing (1.25). The time of tiller emergence from its parent tiller was nearly equal or slightly shorter than that expected from synchronous growth, with a maximum of 0.75 phyllochron at RTP5 in TO1 (Figure 10). The pattern of fluctuation in HS-delay was similar in early and middle but not in late sowing.

Because HS_{ms}-RA measures the difference between HS_{ms} and HS_t, HS_{ms}-RA, and HS-delay in TO1 give the same results (i.e. Figures 10(a) and 11(a) shows the same results except that there is a gap of 2 between HS_{ms}-RA and HS-delay). The HS_{ms}-RA values of most tillers were negative except TO1 at RTP 3 (0.03) and TO2 at RTP 5 (0.06) in late sowing, indicating that the time of tiller emergence was nearly equal to or earlier than the time expected from synchronous growth (Figure 11). HS_{ms}-RA tended to decrease with an increase in the order and position of tillers. The lowest HS_{ms}-RA was TO3 at RTP 10 in early sowing, indicating that this tiller emerged 2.18 phyllochron earlier in HS_{ms} than expected from synchronous growth (Figure 11). The patterns of fluctuation in HS_{ms}-RA were similar in early and middle but not in late sowing (Figure 11).

Table 4. Phyllochron [(°Cd) leaf^{-1})] of tillers in widely spaced wheat sown on different dates.

TO	RTP	Tiller	Early sowing	Middle sowing	Late sowing
		MS	83.8 d†	78.5 c	66.6 ab
1	3	T1	92.0 bcd	77.8 c	78.6 a
	4	T2	88.8 cd	87.9 c	80.5 a
	5	T3	90.2 cd	89.2 c	85.5 a
	6	T4	100.8 abcd	95.9 bc	87.5 a
	7	T5	114.8 a	103.8 abc	
2	5	T10	91.0 cd	83.5 c	78.5 a
	6	T11	100.1 abcd	92.7 bc	81.0 a
		T20	90.2 cd	93.9 bc	81.9 a
	7	T12	103.1 abc	106.6 abc	
		T21	99.0 abcd	98.2 bc	84.3 a
		T30	95.9 bcd	96.7 bc	87.0 a
	8	T13	101.4 abcd		
		T22	104.2 abc		
		T31	103.1 abc	132.1 a	
		T40	109.5 ab	128.4 ab	

TO, tiller order; RTP, relative tiller position.
†Means followed by the different letter within a column are significantly different between tillers by Tukey's HSD ($p < 0.05$).

Final leaf number and number of spikelets per spike

The final leaf number of MS were same for all sowing dates, and they were the largest among the tillers within a plant (Figure 12). The final leaf number of tillers were progressively decreased with an increase of the order and position of tillers, and those in early sowing was

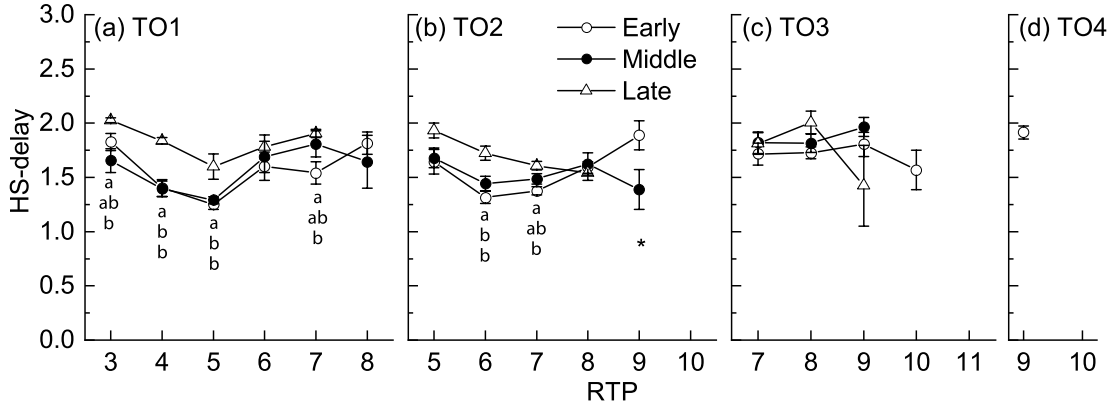


Figure 10. HS-delay of tillers classified by the tiller order (TO) and relative tiller position (RTP). The timing of the calculation of HS-delay was at the first measurement of leaf blade length after the appearance of the leaf ligule of the first leaf of the tiller. Data points are means and error bars represent standard error of the mean. Number of data points for the mean varied according to the order and position of tillers. Different letters below the symbols indicate significant differences among sowing dates by Tukey's HSD ($p < 0.05$). Letter order corresponds to the vertical positions of the symbols within the same RTP. * in (b) indicates significant difference between sowing date by *t*-test ($p < 0.05$).

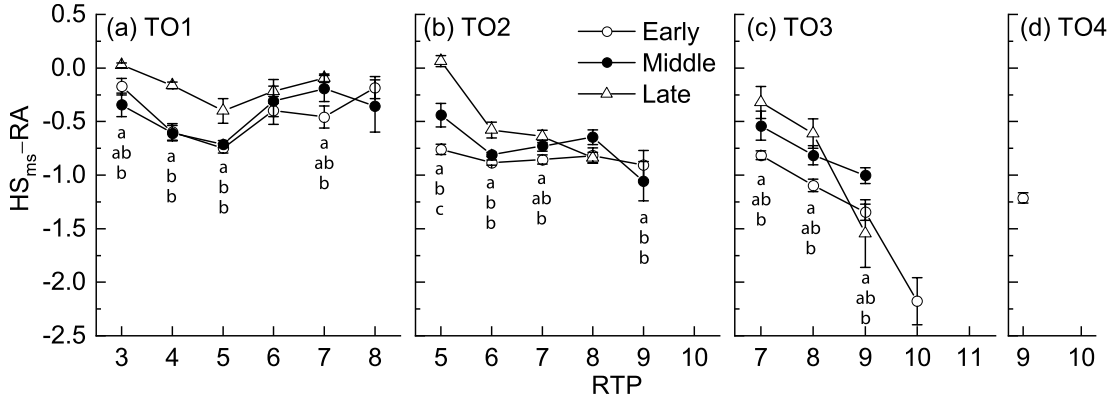


Figure 11. HS_{ms}-RA (difference between HS_{ms} and HS_t) of tillers classified by the tiller order (TO) and relative tiller position (RTP). The timing of the calculation of HS_{ms}-RA was at the first measurement of leaf blade length after the appearance of the leaf ligule of the first leaf of the tiller. Data points are means and error bars represent standard error of the mean. Number of data points for the mean varied according to the order and position of tillers. Different letters below the symbols indicate significant differences among sowing dates by Tukey's HSD ($p < 0.05$). Letter order corresponds to the vertical positions of the symbols within the same RTP.

significantly larger than in middle sowing. However, there were no clear differences on the final leaf number between different tiller order in RTP 7 or higher. Synchronous growth estimates the final leaf number of a tillers as the difference in final leaf number of MS and RTP of the tiller. The final leaf number of all tiller were larger than the final leaf number expected from synchronous growth except TO1 at RTP 3 and RTP 5 in middle sowing (Figure 12).

The number of spikelet per spike was significantly larger in early sowing than in middle and late sowing in most tillers (Figure 13). The number of spikelets per spike in MS was not the largest among the tillers within a plant. In contrast to the progressive decrease of final leaf number with increase of RTP and tiller order, the number of spikelet per spike was not differed in MS and the tillers in TO1 at RTP 3–7, TO2 at RTP 5–8.

Discussion

Although many studies have been published on leaf and tiller development using the phyllochron and site filling in wheat grown at commercial population densities, the mechanisms of synchronous and convergent development among a large number of productive tillers within a widely spaced planted wheat are scarcely documented. Our experiment differs from the experiment with the wide range of sowing dates (Hay, 1986; Manupeerapan & Pearson,

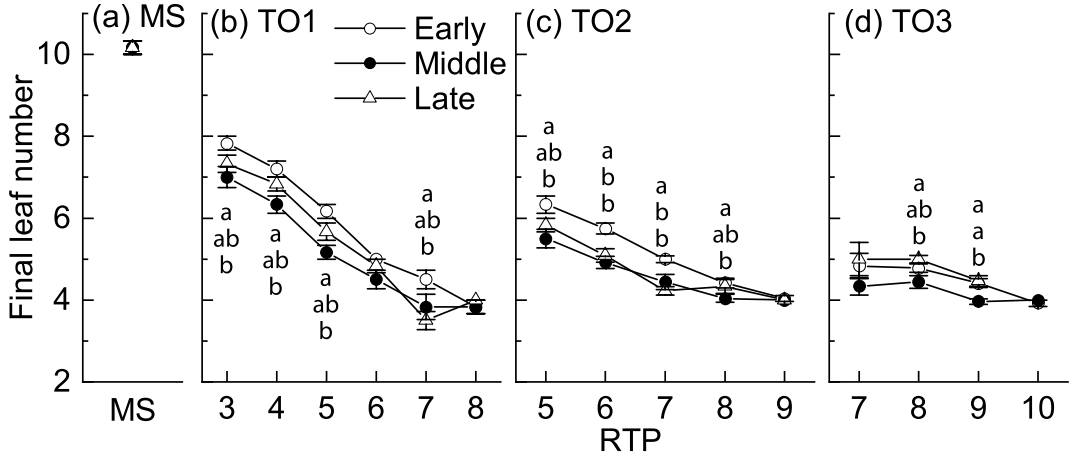


Figure 12. Final leaf number of tillers classified by the tiller order (TO) and relative tiller position (RTP). Data points are means and error bars represent standard error of the mean. Number of data points for the mean varied according to the order and position of tillers. Different letters above or below the symbols indicate significant differences among sowing dates by Tukey's HSD ($p < 0.05$). Letter order corresponds to the vertical positions of the symbols within the same RTP.

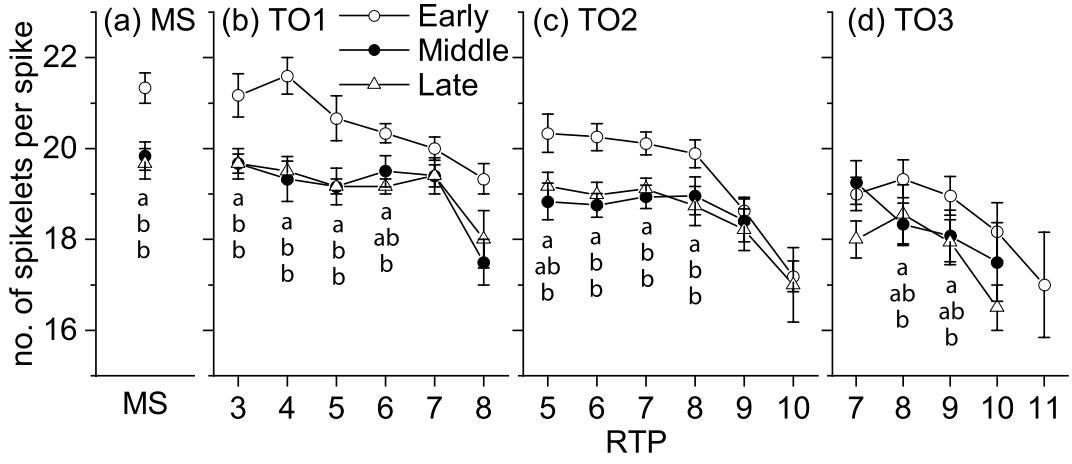


Figure 13. Number of spikelets per spike classified by the tiller order (TO) and relative tiller position (RTP). Data points are means and error bars represent standard error of the mean. Number of data points for the mean varied according to the order and position of tillers. Different letters below the symbols indicate significant differences among sowing dates by Tukey's HSD ($p < 0.05$). Letter order corresponds to the vertical positions of the symbols within the same RTP.

1993) in that the range of sowing time was narrow and the number of tillers per plant is much large. However, there would be similar mechanism that underlie the convergent development between our study and previous studies.

Tiller number dynamics and site filling

In the present study, the number of tillers per plant was significantly decreased by the delay in sowing, whereas the final leaf number on MS was not affected (Table 1). We attributed the decrease in tiller number to a decline in the percentage of tiller emergence at RTP 8 and above (Figure 3). Using the Richards model [4], we revealed graphically that the increase in tiller number with pseudo HS_{ms} slowed and the difference among sowing dates became apparent at about pseudo HS_{ms} 8.6 (Figure 7). The piecewise regression model provided quantitative evidence that the tiller number increased at nearly the same rate as the theoretical rate expected from synchronous growth (site filling = 0.481) until HS_{ms} 8.6, on average, and after the breakpoint site filling was higher in the early and middle than in late sowing (Table 3, Figure 8).

Phyllochron

The relationship between the number of leaves and GDD may be either linear (Baker et al., 1980; Dreccer

et al., 2013) or bilinear (Hay & Delecolle, 1989; Miralles et al., 2001; Ochagavía et al., 2017). In our study, the relationships between HS and GDD was linear regardless of sowing time (Figure 6). This means the phyllochron may vary by sowing date, but it is constant from emergence to the appearance of final leaf. The phyllochron of MS is the shortest or second shortest among tillers within a plant and it gradually became longer with increasing the order and position of tillers in early and middle sowing (Table 4, Figure 9), but we did not find any regularity in the difference of phyllochron among tillers. Functional genomics studies largely expand knowledge of controlling flowering (Laurie et al., 2004) and QTL controlling phyllochron were identified in rice (Miyamoto et al., 2004) and in durum wheat (Sanna et al., 2014). Our results, however, suggested that precise estimation of the phyllochron under various environmental conditions is still difficult.

Timing of tiller emergence and the difference from synchronous growth

The first objective of this study was to explore whether the emergence of individual tillers coincides with the timing expected from synchronous growth and if not, what regularity enables the number of tiller emergence follows the Fibonacci series. For these purposes, we evaluate the synchrony of the time of tiller emergence using the HS-delay and HS_{ms}-RA indices, which measure the difference between the HS of a tiller and the HS of its parent tiller or HS_{ms}, respectively. The former index measures the difference in the time for every axillary node and the latter represents the time difference from a standard expected from synchronous growth. Both indices showed that the time of emergence of tillers was always earlier than the time that expected from synchronous growth (Figures 10 and 11). Although the differences in HS-delay were small, but their accumulation resulted in a larger difference in HS_{ms}-RA. The maximum difference of the time of emergence from the time expected from synchronous growth was 0.75 phyllochron in HS-delay (Figure 10) and 2.18 in HS_{ms}-RA (Figure 11). Thus time of tiller emergence was always earlier than the time expected from synchronous growth, and phyllochron tended to be longer with increasing tiller order and RTP. The trade-off between early timing of tiller emergence and longer phyllochron would enable the number of tiller emergence to follow the Fibonacci series. The pattern of fluctuation in HS-delay and HS_{ms}-RA was similar in early and middle but not in late sowing, however, there were no clear regularity in the differences of HS-delay and HS_{ms}-RA among the tillers.

Convergent development to heading

The second objective of this study was to elucidate the mechanisms that underlie the linear relationship between the number of days from emergence to heading of tillers and the time of their emergence expressed as day of year (Figure 5(a)).

This convergence of development within and between plants should be accompanied by a progressive shortening of the phyllochron (acceleration of leaf appearance rate) or a decrease in the number of organs such as final leaf number and the number of spikelets per spike (Figures 12 and 13). Stern and Kirby (1979) showed that the rate of spikelet initiation increased and the duration decreased with later sowing. Our previous study showed that the rate of initiation in leaf decreased, but that in spikelet increased, and the duration of spikelet initiation phase decreased by the delay of sowing (Toyota et al., 2004).

Our results, however, showed that the phyllochron of MS was the shortest or second shortest among tillers within a plant and it gradually became longer with increasing the order and position of tillers within a plant, although the differences were not significant except for some tillers higher than RTP 7 (Table 4, Figure 9). These results are consistent with those of Bos and Neuteboom (1998), who reported a longer phyllochron in T0, T1, T2 than in MS, and Li and Yamazaki (1994), who showed slower leaf appearance rate in tillers than in MS. In our study, the phyllochron seemed to have counteract effect to shortening of the number of days to heading. On the other hand, a progressive decrease in the final leaf number (Figure 12) and in the number of spikelets per spike (Figure 13) with the increase in the order and position of tillers within a plant may contribute considerably to the convergence to heading time.

Conclusion

Widely spaced planting density produced many productive tillers per plant and different sowing date expand further the variation of the time of emergence and heading. We analyzed the dynamics of leaf and tiller emergence and development using phyllochron, site filling, and indices associated with 'the synchronous growth'.

The number of tillers per plant was significantly decreased by the delay in sowing, while the number of

tiller emergence per phyllochron was almost consistent with that expected from synchronous growth for all sowing dates until HS_{ms} 8.6, on average. The time of tiller emergence was always earlier than the time expected from synchronous growth, and phyllochron tended to be longer with increasing the order and position of tillers. The trade-off between the early timing of tiller emergence and the longer phyllochron would contribute to the number of tiller emergence follows the Fibonacci series. However, we did not find any regularity on the deviation in the time of tiller emergence or fluctuation of phyllochron in individual tillers.

A very close negative linear relationship was found between the number of days from emergence to heading of tillers and the time of their emergence expressed as day of year regardless of the tiller order, position, and sowing date. Although the phyllochron gradually became longer, a progressive decrease of the leaf and spikelet per spike with the increase in the order and position of tillers may contribute considerably to the convergence to heading time. Coordination between the phyllochron and the degree of reduction in the number of organs per tiller seemed to be strongly influenced by the time of their emergence.

Disclosure statement

No potential conflict of interest was reported by the authors.

References

Abichou, M., Fournier, C., Dornbusch, T., Chambon, C., De Solan, B., Gouache, D., & Andrieu, B. (2018). Parameterising wheat leaf and tiller dynamics for faithful reconstruction of wheat plants by structural plant models. *Field Crops Research*, *218*, 213–230. https://doi.org/10.1016/j.fcr.2018.01.010

Alzueta, I., Abeledo, L. G., Mignone, C. M., & Miralles, D. J. (2012). Differences between wheat and barley in leaf and tillering coordination under contrasting nitrogen and sulfur conditions. *European Journal of Agronomy*, *41*, 92–102. https://doi.org/10.1016/j.eja.2012.04.002

Baker, C. K., Gallagher, J. N., & Monteith, J. L. (1980). Daylength change and leaf appearance in winter wheat. *Plant, Cell & Environment*, *3*, 285–287.

Ballaré, C. L., & Casal, J. J. (2000). Light signals perceived by crop and weed plants. *Field Crops Research*, *67*(2), 149–160. https://doi.org/10.1016/S0378-4290(00)00090-3

Baumont, M., Parent, B., Manceau, L., Brown, H. E., Driever, S. M., Muller, B., & Martre, P. (2019). Experimental and modeling evidence of carbon limitation of leaf appearance rate for spring and winter wheat. *Journal of Experimental Botany*, *70*(9), 2449–2462. https://doi.org/10.1093/jxb/erz012

Bos, H. J., & Neuteboom, J. H. (1998). Morphological analysis of leaf and tiller number dynamics of wheat (*Triticum aestivum*L.): Responses to temperature and light intensity. *Annals of Botany*, *81*(1), 131–139. https://doi.org/10.1006/anbo.1997.0531

Cao, W., & Moss, D. N. (1994). Sensitivity of winter wheat phyllochron to environmental changes. *Agronomy Journal*, *86*(1), 63–66. https://doi.org/10.2134/agronj1994.00021962008600010012x

Davies, A. (1974). Leaf tissue remaining after cutting and regrowth in perennial ryegrass. *Journal of Agricultural Science, Cambridge*, *82*(1), 165–172. https://doi.org/10.1017/S0021859600050334

Dreccer, M. F., Chapman, S. C., Rattey, A. R., Neal, J., Song, Y., Christopher, J. T., & Reynolds, M. (2013). Developmental and growth controls of tillering and water-soluble carbohydrate accumulation in contrasting wheat *Triticum aestivum* L.) genotypes: Can we dissect them? *Journal of Experimental Botany*, *64*(1), 143–160. https://doi.org/10.1093/jxb/ers317

Evers, J. B., Vos, J., Andrieu, B., & Struik, P. C. (2006). Cessation of tillering in spring wheat in relation to light interception and red: Far-red ratio. *Annals of Botany*, *97*(4), 649–658. https://doi.org/10.1093/aob/mcl020

Evers, J. B., Vos, J., Fournier, C., Andrieu, B., Chelle, M., & Struik, P. C. (2007). An architectural model of spring wheat: Evaluation of the effects of population density and shading on model parameterization and performance. *Ecological Modelling*, *200*(3–4), 308–320. https://doi.org/10.1016/j.ecolmodel.2006.07.042

Gautier, H., Varlet-Grancher, C., & Hazard, L. (1999). Tillering responses to the light environment and to defoliation in populations of perennial ryegrass (*Lolium perenne*L.) selected for contrasting leaf length. *Annals of Botany*, *83*(4), 423–429. https://doi.org/10.1006/anbo.1998.0840

Goto, Y., & Hoshikawa, K. (1988). Tillering behavior in *Oryza sativa* L. 1 Growth correlatin between the main stem and tillers. *Japanese Journal of Crop Science*, *57* (3), 496–504. In Japanese with English abstract. https://doi.org/10.1626/jcs.57.496

Goto, Y., & Hoshikawa, K. (1989). Tillering behavior in *Oryza sativa* L III. The pattern and the relative rate of increase in tiller number.. *Japanese Journal of Crop Science*, *58* (1), 60–67. In Japanese with English abstract. https://doi.org/10.1626/jcs.58.60

Hanada, K. (1993). Morphology and development of vegetative organs. 4. Tillers. In T. Matsuo & K. Hoshikawa (Eds.), *Science of the rice plant, Volume 1: Morphology* (pp. 165–177). Food and Agriculture Policy Research Center.

Haun, J. R. (1975). Visual quantification of wheat development. *Agronomy Journal*, *65*(1), 116–119. https://doi.org/10.2134/agronj1973.00021962006500010035x

Hay, R. K. M. (1986). Sowing date and the relationships between plant and apex development in winter cereals. *Field Crops Research*, *14*, 321–337. https://doi.org/10.1016/0378-4290(86)90067-5

Hay, R. K. M., & Delecolle, R. (1989). The setting of rates of development of wheat plants at crop emergence: Influence of the environment on rates of leaf appearance. *Annals of Applied Biology*, *115*(2), 333–342. https://doi.org/10.1111/j.1744-7348.1989.tb03392.x

Hay, R. K. M., & Kirby, E. J. M. (1991). Convergence and synchrony - a review of the coodination of development in

wheat. *Australian Journal of Agricultural Science*, *42*(5), 661–700. https://doi.org/10.1071/AR9910661

Katayama, T. (1951). *Studies on tillering in rice, wheat and barley*. Yokendo. In Japanese.

Kirby, E. J. M., Appleyard, M., & Fellowes, G. (1985). Leaf emergence and tillering in barley and wheat. *Agronomie*, *5*(3), 193–200. https://doi.org/10.1051/agro:19850301

Klepper, B., Rickman, R. W., & Belford, R. K. (1983). Leaf and tiller identification on wheat plants 1. *Crop Science*, *23*(5), 1002–1004. https://doi.org/10.2135/cropsci1983.0011183X002300050045x

Klepper, B., Rickman, R. W., & Peterson, C. M. (1982). Quantitative characterization of vegetative development in small cereal grains. *Agronomy Journal*, *74*(5), 789–792. https://doi.org/10.2134/agronj1982.00021962007400050005x

Laurie, D. A., Griffiths, S., Dunford, R. P., Christodoulou, V., Taylor, S. A., Cockram, J., Beales, J., & Turner, A. (2004). Comparative genetic approaches to the identification of flowering time genes in temperate cereals. *Field Crops Research*, *90*(1), 87–99. https://doi.org/10.1016/j.fcr.2004.07.007

Li, J. M., & Yamazaki, K. (1994). Studies on growth and development of tillers in wheat: III. Developmental properties of tillers and their servival. *Japanese Journal of Crop Science*, *63*(3), 460–466. https://doi.org/10.1626/jcs.63.460

Longnecker, N., Kirby, E. J. M., & Robson, A. (1993). Leaf emergence, tiller growth, and apical development of nitrogen-deficient spring wheat. *Crop Science*, *33*(1), 154–160. https://doi.org/10.2135/cropsci1993.0011183X003300010028x

Manupeerapan, T., & Pearson, C. J. (1993). Apex size, flowering and grain yield of wheat as affected by sowing date. *Field Crops Research*, *32*(1–2), 41–57. https://doi.org/10.1016/0378-4290(93)90020-N

McMaster, G. S. (2005). Phytomers, phyllochrons, phenology and temperate cereal development. *The Journal of Agricultural Science*, *143*(2–3), 137–150. https://doi.org/10.1017/S0021859605005083

Miralles, D. J., Ferro, B. C., & Slafer, G. A. (2001). Developmental responses to sowing date in wheat, barley and rapeseed. *Field Crops Research*, *71*(3), 211–223. https://doi.org/10.1016/S0378-4290(01)00161-7

Miyamoto, N., Goto, Y., Matsui, M., Ukai, Y., Morita, M., & Nemoto, K. (2004). Quantitative trait loci for phyllochron and tillering in rice. *TAG Theoretical and Applied Genetics*, *109*(4), 700–706. https://doi.org/10.1007/s00122-004-1690-0

Mulholland, B. J., Craigon, J., Black, C. R., Stokes, D. T., Zhang, P., Colls, J. J., & Atherton, J. G. (1997). Timing of critical developmental stages and leaf production in field-grown spring wheat for use in crop models. *The Journal of Agricultural Science, Cambridge*, *129*(2), 155–161. https://doi.org/10.1017/S0021859697004620

Neuteboom, J. H., & Lantinga, E. A. (1989). Tillering potential and relationship between leaf and tiller production in perennial ryegrass. *Annals of Botany*, *63*(2), 265–270. https://doi.org/10.1093/oxfordjournals.aob.a087741

Ochagavía, H., Prieto, P., Savin, R., Griffiths, S., & Slafer, G. A. (2017). Duration of developmental phases, and dynamics of leaf appearance and tillering, as affected by source and doses of photoperiod insensitivity alleles in wheat under field conditions. *Field Crops Research*, *214*, 45–55. https://doi.org/10.1016/j.fcr.2017.08.015

Percival, J. (1921). Chapter VI The stems. In *The wheat plant; a monograph* (pp. 62–99). London: Duckworth and Co.

Peterson, C. M., Klepper, B., & Rickman, R. W. (1982). Tiller development at the coleoptilar node in winter wheat. *Agronomy Journal*, *74*(5), 781–784. https://doi.org/10.2134/agronj1982.00021962007400050003x

Rawson, H. (1971). Tillering patterns in wheat with special reference to the shoot at the coleoptile node. *Australian Journal of Biological Sciences*, *24*(4), 829–842. https://doi.org/10.1071/BI9710829

Richards, F. J. (1959). A flexible growth function for empirical use. *Journal of Experimental Botany*, *10*(2), 290–300. https://doi.org/10.1093/jxb/10.2.290

Sanna, G., Giunta, F., Motzo, R., Mastrangelo, A. M., & De Vita, P. (2014). Genetic variation for the duration of pre-anthesis development in durum wheat and its interaction with vernalization treatment and photoperiod. *Journal of Experimental Botany*, *65*(12), 3177–3188. https://doi.org/10.1093/jxb/eru170

Skinner, R. H., & Nelson, C. J. (1992). Estimation of potential tiller production and site usage during tall fescue canopy development. *Annals of Botany*, *70*(6), 493–499. https://doi.org/10.1093/oxfordjournals.aob.a088509

Sparkes, D. L., Holme, S. J., & Gaju, O. (2006). Does light quality initiate tiller death in wheat? *European Journal of Agronomy*, *24*(3), 212–217. https://doi.org/10.1016/j.eja.2005.08.003

Stern, W. R., & Kirby, E. J. M. (1979). Primordium initiation at the shoot apex in four contrasting varieties of spring wheat in response to sowing date. *The Journal of Agricultural Science, Cambridge*, *93*(1), 203–215. https://doi.org/10.1017/S0021859600086299

Toms, J. D., & Lesperance, M. L. (2003). Piecewise regression: A tool for identifying ecological thresholds. *Ecology*, *84*(8), 2034–2041. https://doi.org/10.1890/02-0472

Toyota, M., Kobayashi, Y., Miyoshi, Y., Yasumura, N., Kusutani, A., & Asanuma, K. (2004). Variation in the determination of leaf, spikelet and floret number on the main stem of wheat with sowing dates. *Japanese Journal of Crop Science*, *73* (1), 10–17. In Japanese with English abstract. https://doi.org/10.1626/jcs.73.10

Toyota, M., Tatewaki, N., Morokuma, M., & Kusutani, A. (2014). Tillering responses to high red/far-red ratio of four Japanese wheat cultivars. *Plant Production Science*, *17*(2), 124–130. https://doi.org/10.1626/pps.17.124

Wilhelm, W. W., & McMaster, G. S. (1995). Importance of the phyllochron in studying development and growth in grasses. *Crop Science*, *35*(1), 1–3. https://doi.org/10.2135/cropsci1995.0011183X003500010001x