



## Morphological Analysis of Leaf and Tiller Number Dynamics of Wheat (*Triticum aestivum* L.): Responses to Temperature and Light Intensity

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In recent literature on Gramineae species, leaf and tiller number dynamics have been studied by analysing site filling and the phyllochron of the mainstem. However, site filling is influenced by three components: (1) the phyllochron of the mainstem and daughter tillers; (2) specific site usage (i.e. fraction of buds that ultimately develop into a visible tiller at a specific site); and (3) HS-delay (i.e. difference in Haun Stage (HS) between the parent tiller and daughter tiller above the point where the daughter tiller appears). These three morphological components affecting site filling were studied under different environmental conditions in a growth chamber experiment with spring and winter wheat (*Triticum aestivum* L.). Treatments were temperature (daily average 10.5, 15.5 or 20.5 °C) and light intensity (111, 191 or 286  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ). Effects of temperature and light intensity on phyllochron were well described by equations already reported in the literature. Specific site usage was higher at cooler temperatures and greater light intensities and was related to tiller position. It is proposed that these effects on specific site usage reflect differences in availability of local assimilate for tiller appearance. HS-delay of a tiller was shorter if the expected tiller appearance was later and was only slightly affected by light intensity or temperature. This new concept, combining HS-delay and specific site usage, can be useful in constructing more general models of the effects of environmental factors on the dynamics of leaf number and leaf area of Gramineae species. © 1998 Annals of Botany Company

**Key words:** *Triticum aestivum*, wheat, phyllochron, temperature, light intensity, leaf number, tillering, site filling, site usage.

### INTRODUCTION

To model crop growth and potential dry matter production an adequate simulation of leaf area dynamics is a prerequisite (Goudriaan and Van Laar, 1994), particularly in the early stages of crop development when the canopy is still open. An adequate simulation of leaf area dynamics is also needed for realistic simulation of crop-weed competition (Kropff, 1993; Lotz *et al.*, 1996), since, especially during early development, the rate of leaf area increase can be very decisive for establishment and growth of weeds.

Leaf number dynamics are determined by the birth and death rates of leaves (Harper, 1989). In early crop growth, leaf number dynamics are determined predominantly by the appearance of new leaves, which is a function of tiller appearance and leaf appearance per tiller. To model leaf production successfully, both processes should be analysed.

In some models for cereal crop growth, tillering has been calculated from the leaf appearance rate of the mainstem, using a fixed pattern of tiller production, based on the Fibonacci series (Porter, 1985; Boone, Rickman and Whisler, 1990). However, in recent literature on grasses for productive grassland (Van Loo, 1992), tillering is calculated from leaf appearance rate and site filling (Davies, 1974; Neuteboom and Lantinga, 1989). Site filling, expressed in tillers per tiller per day, varies under the influence of environmental conditions and is therefore more appropriate for dynamic simulation. Since, in this approach, leaf

appearance rate is measured on the mainstem only, and site filling is calculated from the total tiller number increase per plant, a third, and even more detailed approach is possible and, for some applications, desirable. In this approach the presence, appearance time and leaf appearance rate should be measured for each individual tiller.

This paper presents data on tillering and leaf number dynamics of wheat from an experiment with spaced plants at different combinations of temperature and light intensity. In a companion paper (Bos and Neuteboom, 1998) areas of individual leaves are analysed. The time of appearance, length and width of every leaf on a plant were recorded and the data were used to determine the time course of leaf and tiller numbers per plant according to: (1) a fixed pattern according to the Fibonacci series; (2) the site filling approach; and (3) a detailed approach to tillering based on the presence, time of appearance and leaf appearance rate of individual tillers. Temperature effects were analysed because temperature has large effects on both phyllochron and tillering (Mitchell, 1953; Cao and Moss, 1989) and it varies greatly under field conditions. Light intensity effects were analysed because a reduction in light intensity below the saturation level for photosynthesis reduces the rate of dry matter production, and relatively low light intensities could also be responsible for variation in tillering when plants are competing for light. The focus of this study was on spring wheat. Since the initiation of reproductive development of spring wheat could possibly reduce tillering, some unvernallized winter wheat plants were also examined.

## MATERIALS AND METHODS

Spring and winter wheat (*Triticum aestivum*) plants were grown in three growth chambers, each with a different temperature (T) regime. Within each growth chamber, three compartments were created with different light intensities (L).

### Plant material and growing conditions

Spring wheat cv. Minaret (mean seed weight 0.045 g) and winter wheat cv. Ritmo (mean seed weight 0.042 g) were sown at 3 cm depth in square 18 × 18 cm (4.5 l) pots filled with a mixture of 33% sandy soil and 67% quartz sand. Three seeds were sown per pot. The pots (540 for spring wheat; 108 for winter wheat) were placed on trolleys in three growth chambers [constant relative humidity 70%; daily photoperiod 0700–2100 h; day temperature (0900–2100 h) 18 °C, night temperature 13 °C].

One day after 50% emergence, plant number per pot and pot number were reduced to obtain a homogeneous population of plants (one plant per pot; 120 pots of spring wheat and 24 of winter wheat per growth chamber). Using white curtains, each growth chamber was divided into three equal compartments (3.20 × 1.50 m) for the L treatments. Each compartment contained 40 spring wheat and 8 winter wheat plants, chosen randomly and arranged uniformly, resulting in an initial plant density of 31 m<sup>-2</sup>. T and L treatments were started on the same day, but the photoperiod and relative humidity remained the same as in the pre-emergence period.

During growth, trolleys were rotated within a compartment at intervals of approx. 0.75 mainstem phyllochrons to minimize variation in conditions for individual plants. The pots were irrigated with tap water at least once a day and nutrient solution (Steiner, 1984) was supplied at intervals of two mainstem phyllochrons in quantities sufficient to meet the expected growth rate and desired high nutrient concentration in the plant material.

### Treatments

The following day/night temperature (T) treatments were imposed at the intermediate light intensity (L2): 13/8 °C (T1); 18/13 °C (T2); and 23/18 °C (T3). These temperatures ensured large differences in the rate of increase in leaf area. The change-over from day to night temperature and *vice versa* occurred within 0.5 h.

Light intensity treatments (L) were established as follows (values with s.e.m.): 111 ± 7 μmol m<sup>-2</sup> s<sup>-1</sup> = 5.6 ± 0.35 mol m<sup>-2</sup> d<sup>-1</sup> (L1); 191 ± 10 μmol m<sup>-2</sup> s<sup>-1</sup> = 9.6 ± 0.50 mol m<sup>-2</sup> d<sup>-1</sup> (L2); and 286 ± 12 μmol m<sup>-2</sup> s<sup>-1</sup> = 14 ± 0.60 mol m<sup>-2</sup> d<sup>-1</sup> (L3). In each compartment, the light ceiling contained six metal halide (Philips HPI 400 W) and six high pressure sodium (Philips AGROSON-T 400 W) lamps. For L3, all lamps were switched on, for L2, eight lamps, and for L1, four lamps. The metal halide lamp/high pressure sodium lamp ratio was 1:1 for every L treatment. Light intensity

was measured as photosynthetic photon flux density (PPF) using a LI-190 SA Quantum Sensor at nine points per compartment, just above the pots. The heights of the trolleys were adjusted to ensure required PPF values were attained.

On average, the air temperature was 0.5 °C higher in L3 and 0.5 °C lower in L1 than in L2 during the light period. During the dark period air temperatures were the same.

### Measurements

Destructive measurements were done only on spring wheat plants. Eight plants per treatment were harvested at intervals of one mainstem phyllochron, starting from tip appearance of leaf 4 up to tip appearance of leaf 8 (five harvests). After each harvest, the remaining pots were rearranged to minimize interplant competition (plant density at last harvest was 10 m<sup>-2</sup>). At each harvest, seven plants were separated into roots and shoots, the shoot into individual tillers, and each tiller into separate visible leaves and internodes/sheaths. The dry weight of each component was measured after drying to constant weight at 70 °C.

For winter wheat, the number of leaves and the length of the youngest and second youngest visible leaves were measured non-destructively for each tiller in the T2 treatments on the same day that the spring wheat plants were harvested in that treatment (five times). Unintentionally, these measurements were not made at the first harvest of treatment T2L2, and, in the T1 and T3 treatments, they were made only at the last harvest of the spring wheat plants.

### Definitions and calculations

*General outline of calculations.* To compare tiller numbers per plant according to the three models, leaf stages have to be defined, and a leaf- and tiller-identification system is needed. The leaf stage of a tiller was measured as the Haun Stage (Haun, 1973) and tillers and leaves were identified according to the system of Klepper, Rickman and Peterson (1982). The equation of Volk and Bugbee (1991) was used to calculate the effects of light intensity on the interval between the appearance of successive leaves on a tiller (the phyllochron). For the site filling model, the maximum number of tillers can be calculated, and the theoretical total leaf number per plant (all stems) can be calculated from an equation developed by Neuteboom and Lantinga (1989) and amplified by Van Loo (1992). In discussing leaf and tiller identification, two patterns of tillering (plant types 1 and 2) are considered (see below).

*Leaf stage.* The leaf stage of tiller (t), measured as Haun Stage (HS<sub>t</sub>), is:

$$HS_t = \text{Number of visible leaves on tiller } t - 1 + \frac{\text{Length of youngest visible leaf}}{\text{Length of } 2^{\text{nd}} \text{ youngest visible leaf}} \quad (1)$$

*Tiller and leaf identification.* Tillers and leaves were

TABLE 1. Parent tiller and quantitative parameters for selected tiller types

Tiller type	Parent tiller	Parameters related to plant development stage		Parameters related to position in a plant		
		HS <sub>ms</sub> at tiller appearance (according to plant type 1)	HS <sub>ms</sub> at tiller appearance (according to plant type 2)	Tiller order	Tiller position on parent tiller	Summed tiller position
t0	ms	1	2	1	0	0
t0.0	t0	2	4	2	0	0
t0.0.0	t0.0	3	6	3	0	0
t0.1	t0	3	5	2	1	1
t1	ms	2	3	1	1	1
t1.0	t1	3	5	2	0	1
t2	ms	3	4	1	2	2

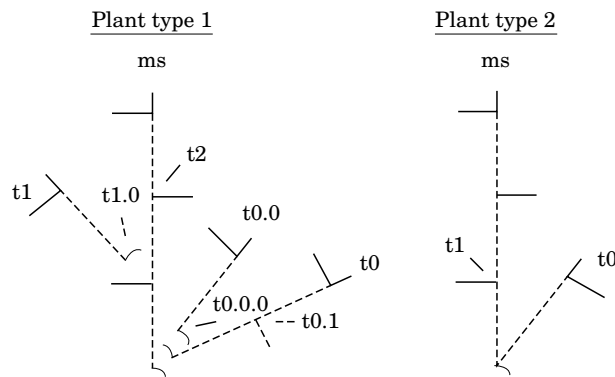


FIG. 1. Potential tillering pattern according to plant type 1 or 2 during the elongation of the fourth mainstem leaf. Details of each pattern are explained in the text. Dashed lines indicate leaf sheaths, solid lines visible leaf blades, and brackets prophylls.

identified according to the system of Klepper *et al.* (1982), by counting the leaves acropetally, the coleoptile or prophyll being named l0 and the first foliar leaf l1. The seedling stem was the mainstem (ms). Other tillers were named after their parent leaf, e.g. t0 was the tiller from the axil of l0. Higher-order tillers were indicated by additional digits; for example, t1.0 was the tiller from the axil of l1.0, the prophyll of t1 (Fig. 1; plant types 1 and 2 are discussed below). Tiller t1.0 was the ‘daughter’ tiller of t1, which in turn was its ‘parent’ tiller. This system identifies each tiller specifically, but can only be used to analyse effects of tiller type as a qualitative parameter. To analyse effects of tiller type as a quantitative parameter, five parameters were calculated for every tiller type (Table 1). The leaf stage of the mainstem (HS<sub>ms</sub>) at tiller appearance, according to plant type 1 or 2 (Fig. 1), was used to test whether effects of tiller type were related to plant development stage. Tiller order (i.e. primary, secondary, tertiary etc.), tiller position on parent tiller and summed tiller position (i.e. sum of all numbers in the designation of the tiller, e.g. for t1.3.0 this is 1 + 3 + 0 = 4) were calculated to test whether effects of tiller type were related to position on a plant.

**Phyllochron.** Phyllochron for each tiller was expressed in degree-days using a base temperature of 0 °C, and was calculated by linear regression of thermal time *vs.* HS<sub>i</sub>. The

effects of light intensity were evaluated using the equation (Volk and Bugbee, 1991):

Phyllochron

$$= \text{Phyllochron}_{\min} \frac{(\text{PPF}_{\text{hf}} + \text{PPF} - 2 \times \text{PPF}_{\min})}{(\text{PPF} - \text{PPF}_{\min})} \quad (2)$$

where PPF is the daily photosynthetic photon flux (mol m<sup>-2</sup> d<sup>-1</sup>), PPF<sub>min</sub> the minimum PPF for leaf appearance [= 2 mol m<sup>-2</sup> d<sup>-1</sup> (Volk and Bugbee, 1991)], PPF<sub>hf</sub> the PPF for half-saturation of leaf appearance rate (mol m<sup>-2</sup> d<sup>-1</sup>) and Phyllochron<sub>min</sub> the minimum phyllochron for PPF → ∞ (°C d). PPF<sub>hf</sub> and Phyllochron<sub>min</sub> were estimated by non-linear regression.

**Site filling method.** The total number of tillers per plant was estimated from the leaf appearance rate of the mainstem, and site filling, which is defined as the number of new tillers per tiller per phyllochron (Davies, 1974). Since Neuteboom and Lantinga (1989) showed that a minimum of one phyllochron separates the appearance of a tiller and its first daughter tiller, maximum site filling is 0.69. Such a maximally-tillering plant is illustrated in Fig. 1 (plant type 1). Site filling was calculated by linear regression of ln(number of tillers per plant) *vs.* HS<sub>ms</sub>.

Leaf number per plant (L<sub>p</sub>) can be calculated from site filling (F<sub>s</sub>) and Haun Stage of the mainstem (HS<sub>ms</sub>) using the equation (Neuteboom and Lantinga, 1989):

$$L_p = e^{nF_s} T_{p,0} (e^{HS_{ms} F_s} - 1) + L_{p,0} \quad (3)$$

where n is the mean number of inhibited buds per tiller and T<sub>p,0</sub> and L<sub>p,0</sub> are the numbers of tillers and leaves, respectively, per plant at day 0. Van Loo (1992) has shown that n depends on F<sub>s</sub>:

$$n = 1 - \frac{\ln(e^{F_s} - 1)}{F_s} \quad (4)$$

Combining eqns (3) and (4) yields a new equation:

$$L_p = e^{F_s - \ln(e^{F_s} - 1)} T_{p,0} (e^{HS_{ms} F_s} - 1) + L_{p,0} \quad (5)$$

**Fibonacci series method.** This method assumes that tiller number increases with leaf number on the mainstem according to the Fibonacci series (1, 1, 2, 3, 5, 8 etc), because

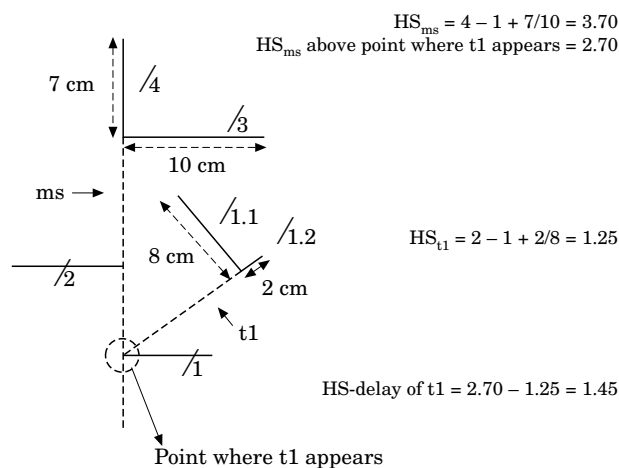


FIG. 2. Illustration of the calculation of  $HS_i$  and  $HS\text{-delay}$ . Leaf sheaths are indicated by dashed lines, leaf blades by solid lines and the lengths of the two youngest leaf blades per tiller are given.

two phyllochrons separate the appearance of a tiller and its first daughter tiller. Site filling for such a plant is 0.49 (Neuteboom and Lantinga, 1989). Plant type 2 in Fig. 1 shows such a plant schematically.

**Detailed method.** This method requires estimates of the phyllochron of individual tillers, the presence of tillers, and the timing of appearance of tillers. Presence of tillers was expressed as 'specific site usage', defined as the fraction of the buds in a specific axil that have ultimately grown out into visible tillers, and was calculated as the number of plants that possessed this tiller divided by the number of plants that possessed its parent tiller, determined at least one phyllochron after the tiller was expected to appear. Data of specific site usage were transformed using a logistic link function, assuming a binomial distribution (McCullagh and Nelder, 1989). To analyse quantitative effects of tiller type for each individual treatment, one of the five quantitative parameters for tiller type (Table 1) was used as independent variable in the regression with the transformed specific site usage as dependent variable.

The timing of appearance of a tiller ( $t$ ) was expressed as 'HS-delay', which is the difference between the HS of tiller  $t$  and the HS of its parent tiller above the leaf from which axil tiller  $t$  appears (equivalent to 'NLAT' in Skinner and Nelson, 1992) (Fig. 2). HS-delay of tiller  $t$  was determined between  $HS_t$  1 and 2. The observed values were compared with the values for plant type 1 and 2 [HS-delay is 1 and 2 respectively (Neuteboom and Lantinga, 1989)]. To analyse quantitative effects of tiller type on HS-delay, a simple equation was assumed:

$$HS\text{-delay} = HS\text{-delay}_{\min} + (HS\text{-delay}_0 - HS\text{-delay}_{\min})e^{-RDR \cdot x} \quad (6)$$

where  $x$  is one of the five quantitative parameters for tiller type (Table 1),  $HS\text{-delay}_{\min}$  the HS-delay for  $x \rightarrow \infty$ ,  $HS\text{-delay}_0$  the HS-delay for  $x = 0$  and  $RDR$  the relative decline rate. Two values of  $HS\text{-delay}_{\min}$  were evaluated: 1 (plant type 1) and 2 (plant type 2). This equation assumes that HS-delay declines with  $x$ , which is based on indications from

the literature (Ito, Nakayama and Tsubota, 1987).  $HS\text{-delay}_0$  and  $RDR$  were estimated by non-linear regression.

In the detailed method, leaf number per plant was calculated simply by daily summation of the number of leaves of all tillers present.

## RESULTS

### Leaf death

Under the particular conditions of this experiment (relatively low irradiance; no competition between plants), there was no leaf death under any treatment by the time of appearance of the tip of leaf 8.

### Phyllochron

For spring wheat, the phyllochron of the mainstem was well fitted by eqn (2) ( $P < 0.05$ ), using values of  $91 \pm 5^\circ\text{C d}$  for  $Phyllochron_{\min}$ , and  $3.5 \pm 0.3 \text{ mol m}^{-2} \text{ d}^{-1}$  for  $PPF_{hr}$  (values with s.e.m.) (Fig. 3). Temperature did not have a significant effect on this relationship. The phyllochrons of tillers  $t_0$ ,  $t_1$  and  $t_2$ , also well fitted by eqn (2), were between 0 and 14% longer than the mainstem phyllochron. However, the phyllochron of  $t_{0.0}$  could not be fitted by eqn (2), and the observed values were very high, between 150 and  $350^\circ\text{C d}$ . The phyllochron of the winter wheat mainstem was, on average, 17% longer than that of spring wheat (data not shown).

### Site filling

In spring wheat, site filling was always below the value for plant type 2 (Fig. 4A) and linear, quadratic or interaction terms of temperature and light intensity did not change site filling significantly ( $P < 0.05$ ). The standard error of the

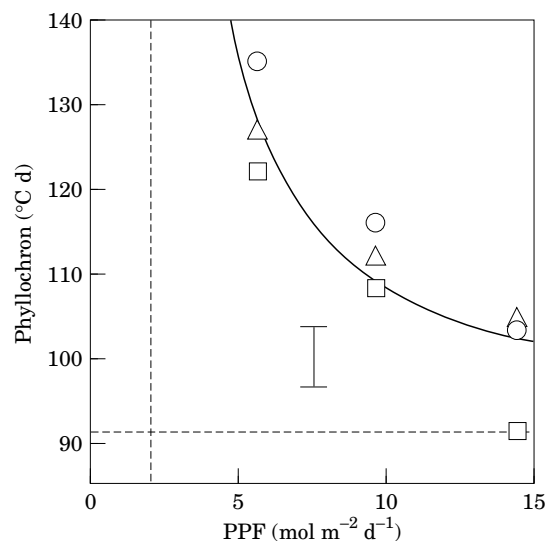


FIG. 3. The phyllochron of the mainstem of spring wheat as a function of PPF, for the three temperature treatments ( $\square$ , T1;  $\circ$ , T2;  $\triangle$ , T3). Dashed lines indicate asymptotes, and the vertical bar indicates twice the s.e.m. of the phyllochron values.

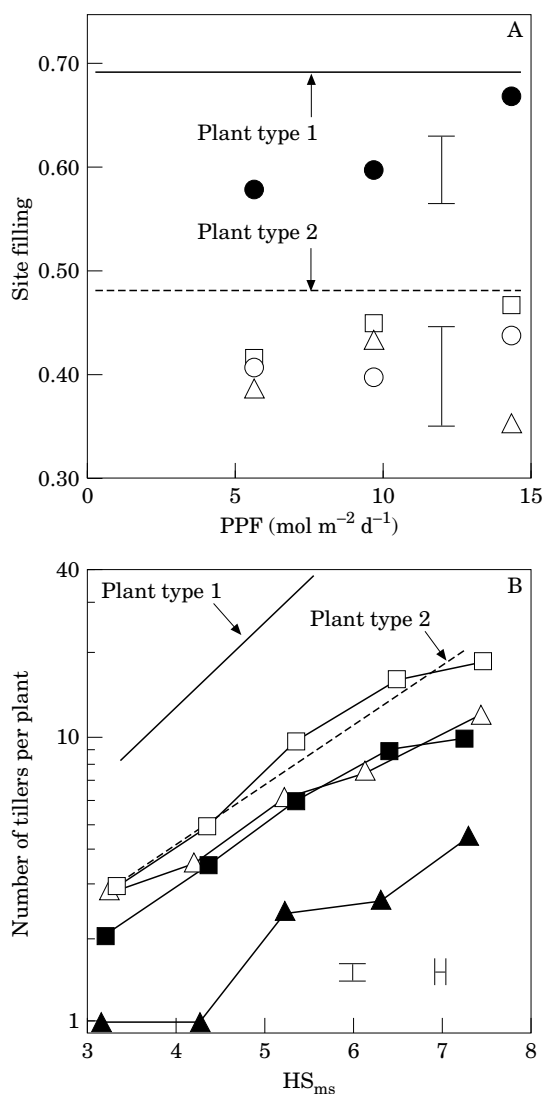


FIG. 4. A, Site filling in spring wheat ( $\square$ , T1;  $\circ$ , T2;  $\triangle$ , T3) and winter wheat ( $\bullet$ , T2) as a function of PPF. B, Number of tillers per plant (log scale) as a function of  $HS_{ms}$  for treatments T1L1 ( $\blacksquare$ ), T1L3 ( $\square$ ), T3L1 ( $\blacktriangle$ ) and T3L3 ( $\triangle$ ) in spring wheat. The maximum tillering patterns of plant type 1 and 2 are indicated, and the vertical and horizontal bars indicate twice the s.e.m. of the data points.

individual points in Fig. 4A is relatively large, owing to the irregular increase in tiller number per plant with  $HS_{ms}$ , as illustrated for four treatments in Fig. 4B. In winter wheat, site filling values reached 0.67, which is close to the value for plant type 1.

#### Detailed method: specific site usage

Tiller type, temperature and light intensity each had a significant and important effect on specific site usage in spring wheat (Fig. 5) and in winter wheat (data not shown). In general, a high specific site usage was observed for low temperatures, high light intensities, high tiller position on the ms ( $t_3 > t_2 > t_1 > t_0$ ) and low tiller order (primary > secondary > tertiary). The five parameters in Table 1 were used as independent variables to quantify tiller

type effects per treatment. For each of the nine treatments, one of the 'position' parameters (tiller order, tiller position on parent tiller or summed tiller position) accounted for most of the variation. For winter wheat, specific site usage of  $t_0$ ,  $t_{0.0}$ ,  $t_{0.1}$  and  $t_1$  was lower than for spring wheat, while for the other tillers specific site usage was higher or equal.

#### Detailed method: HS-delay

There was a large and significant effect of tiller type on HS-delay for both spring and winter wheat, with a clear trend of reduction in HS-delay with higher placement of the tiller on the mainstem, and with higher tiller order. Of the five tiller parameters tested (Table 1),  $HS_{ms}$  at the time the tiller appears (plant type 1) with a  $HS\text{-delay}_{min} = 1$  accounted best for most of the variation in HS-delay using eqn (6) [ $HS\text{-delay} = 2.2 \pm 0.05$  and  $RDR = 0.31 \pm 0.038$  (spring,  $P < 0.05$ );  $2.5 \pm 0.32$  and  $1.2 \pm 0.17$  (winter,  $P < 0.05$ )] (Fig. 6). RDR was much higher for winter wheat than for spring wheat, indicating a quick decline of HS-delay to 1 for winter wheat. Most of the data in Fig. 6 fell below  $HS\text{-delay} = 2$ , the absolute minimum for plant type 2.

For spring wheat, temperature and light intensity showed small but significant effects on HS-delay. These effects were due to three clearly-deviating data points, i.e. T3L3 for tiller  $t_0$ , T2L1 for tiller  $t_1$  and T3L1 for tiller  $t_2$ .

#### Leaf number per plant

To calculate leaf number per plant of spring wheat by the site filling method, eqns (2) and (5) were used with  $Phyllochron_{min} = 91$  °C d,  $PPF_{hr} = 3.5$  mol m<sup>-2</sup> d<sup>-1</sup> and the measured site filling values for each treatment (Fig. 4A). In the detailed method, leaf number per plant was calculated using eqns (2) and (6), with  $Phyllochron_{min} = 91$  °C d and  $PPF_{hr} = 3.5$  mol m<sup>-2</sup> d<sup>-1</sup> for all tillers,  $RDR = 1.22$ ,  $HS\text{-delay}_{min} = 1$ ,  $HS\text{-delay}_0 = 2.15$ , and specific site use values as observed for each treatment and tiller type (Fig. 5). Initial values were taken from the first harvest for each treatment.

Figure 7 compares the resulting lines for each method with experimental data on leaf number per plant on a log scale. The site filling method gives a smooth curve with a decreasing slope for treatments T1L1, T1L3 and T3L3. For treatment T3L1, the slope increases owing to relatively low initial number of tillers compared with initial number of leaves [eqn (5)]. The detailed method shows a discontinuous increase, reflecting the discrete events (leaf and tiller appearance) that are included in this method.

## DISCUSSION

#### Differences between spring and winter wheat

Both spring and winter wheat plants formed new tillers up to the end of the observation period, and showed an increased specific site usage with higher placement of tillers on their parent tiller. It is, therefore, unlikely that the initiation of reproductive development in spring wheat affected the tillering process. However, there were clear

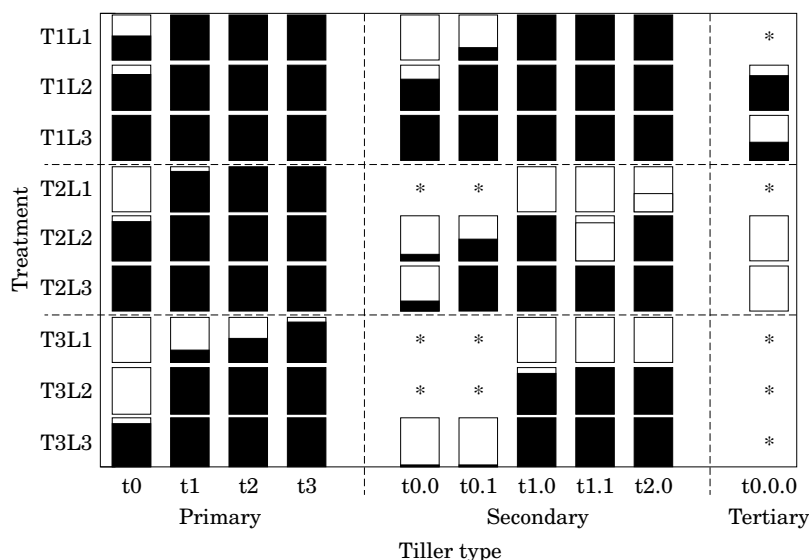


FIG. 5. Specific site usage of different tiller types (primary, secondary and tertiary) for the nine treatments in spring wheat. The proportional filling of each box represents the specific site usage, e.g. specific site usage of t0 is 0 for T2L1 and 1 for T1L3. Asterisks indicate that specific site usage could not be calculated (parent tiller not present).

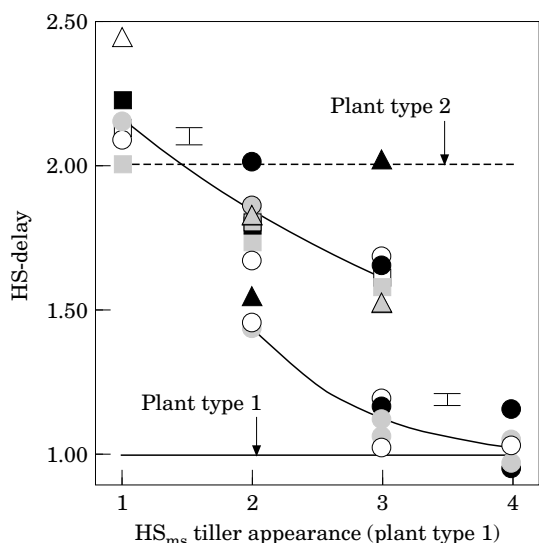


FIG. 6. HS-delay as a function of the quantitative tiller parameter 'HS<sub>ms</sub> at tiller appearance (plant type 1)' calculated for tillers t0, t0.0, t1 and t2 (spring wheat: upper line) or tillers t1, t1.0, t2 and t3 (winter wheat: lower line) for the nine treatments. Symbols for the three temperature treatments are as in Fig. 3, and light intensity treatments are represented by shading: L1 = black; L2 = grey; L3 = white. Vertical bars indicate twice the s.e.m. of the data points.

differences between the two wheat types: spring wheat had shorter phyllochrons, a higher HS-delay and a lower specific site usage, except for the t0 tiller and its daughter tillers. This shows that genotype effects on leaf and tiller number parameters can be substantial.

*Does the Fibonacci series represent the maximum tillering pattern?*

This research has shown that plant type 2 (Fibonacci series; HS-delay = 2) does not represent the type with the

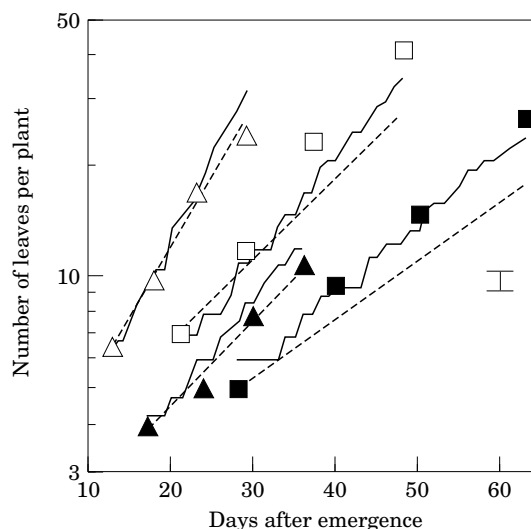


FIG. 7. Increase in number of leaves per plant (log scale) of spring wheat observed for treatments T1L1 (■), T1L3 (□), T3L1 (▲) and T3L3 (△), and predicted by the site filling (---) and the detailed methods (—) (see text). The first harvest was taken as starting point. The vertical bar indicates twice the s.e.m. of the data points.

maximum possible number of tillers. Spring wheat and, more clearly, winter wheat showed much lower HS-delay values, down to 1 (Fig. 6). Therefore, as in perennial ryegrass (Neuteboom and Lantinga, 1989) plant type 1 is more representative of the maximum tillering pattern for wheat. This conclusion seems to conflict with a site filling for spring wheat that was never higher than 0.49 (plant type 2) (Fig. 4A), but site filling is affected by tiller type effects on phyllochron, specific site usage and HS-delay. For example, a decrease of site filling from 0.69 to 0.49 can be due to: (1) a rise in HS-delay from 1 to 2; (2) a decrease in specific site usage of all buds from 1 to 0.63; or (3) an increase from 1 to 2 in the phyllochron of tillers relative to the mainstem. It

was shown that tiller type indeed has an effect on all these three parameters. These confounding effects of tiller type on phyllochron, specific site usage and HS-delay, all three affecting site filling, may have led to the incorrect conclusion that the Fibonacci series represents the maximum site filling pattern for wheat (Boone *et al.*, 1990).

#### Comparison between the site filling and detailed methods

Both the site filling and detailed methods described trends in the number of leaves per plant of the experimental data well (Fig. 7) and both methods can deal with an increasing and decreasing relative growth rate of leaf number in time. Compared with the detailed method, site filling has the strong advantage that the effects of environmental factors need only be measured for two parameters: phyllochron of the mainstem and site filling. However, the site filling method has a number of limitations: (1) site filling is not constant (Fig. 4B); (2) differences in site filling are difficult to interpret since they can be due to effects on the phyllochron of tillers relative to the mainstem, specific site usage and HS-delay of appearing tillers; and (3) because the site filling method does not give information on which tiller types appear, leaf area growth can be included only if leaf area growth is equal for every tiller. Since this is certainly not true (Bos and Neuteboom, 1998), the detailed method is preferred if the regulation of the parameters involved in this method is sufficiently understood.

#### Regulation of phyllochron

The degree-day concept, adjusted for light intensity effects [eqn (2)], fitted the data on phyllochron well, and estimates of  $\text{Phyllochron}_{\min}$  and  $\text{PPF}_{\text{hr}}$  were close to those found previously (McMaster *et al.*, 1991; Volk and Bugbee, 1991). At higher temperatures, the degree-day concept will fail and other equations (e.g. Volk and Bugbee, 1991; Yin *et al.*, 1995) should be used. Tillers t0, t1, t2 had longer phyllochrons than the mainstem, although differences were small, but tiller t0.0 had a much longer phyllochron, which could be related to the unfavourable positions of prophyll and coleoptile tillers, as also found by Kirby, Appleyard and Fellowes (1985) and Skinner and Nelson (1992).

#### Regulation of specific site usage

Specific site usage increased significantly with higher primary tiller position, as also observed for wheat by Rickman, Klepper and Peterson (1985), for barley by Cannell (1969) and for ryegrass by Mitchell (1953). Lower light intensities reduced specific site usage of lower primary tillers in the current experiment, as was also found by Mitchell (1953) and Rickman *et al.* (1985), and higher temperatures reduced site usage, in agreement with the findings of Mitchell (1953) and Cannell (1969). It appears that environmental factors have their greatest impact on specific site usage during early growth. Generally, the following factors have been found to reduce specific site usage: (1) low nutrient availability (Van Loo, Schapendonk and De Vos, 1992); (2) low carbohydrate availability

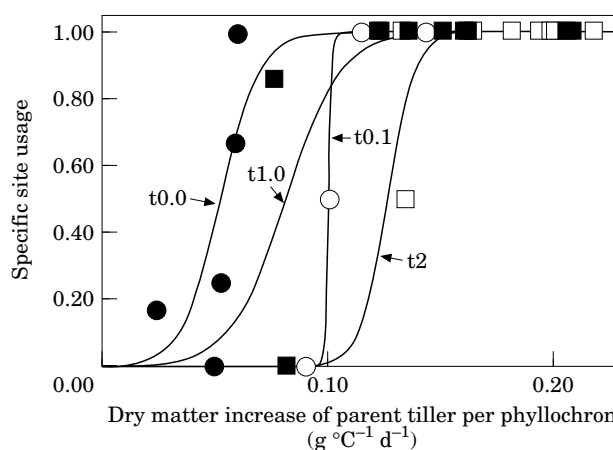


FIG. 8. Specific site usage of four daughter tillers as a function of the total dry matter increase of the parent tiller per phyllochron (see text). For a given tiller, one data point represents a treatment. ●, t0.0; ○, t0.1; ■, t1.0; □, t2. Fitted logistic curves are shown for each tiller type.

(Davies, 1965); and (3) a low red/far-red ratio (Casal, Sanchez and Gibson, 1990). In the current experiment, nutrients were adequately supplied at fixed  $\text{HS}_{\text{ms}}$  and the red/far-red ratio was high ( $> 2$ ). Carbohydrate availability could therefore have been responsible for the observed differences between light and temperature treatments.

Since one of the three 'position' parameters (Table 1) always accounted for most of the variation in specific site usage, plant carbohydrate availability can not explain differences in specific site usage between different tiller types. If carbohydrate availability is the key factor involved, two mechanisms could be responsible for tiller type effects on specific site usage: (1) sinks (e.g. tiller buds) close to the source for carbohydrates (visible leaf blades) have highest priority; (2) the amount of carbohydrates needed for a bud to grow out into a visible tiller differs between buds.

There is evidence that, in wheat, assimilates are translocated preferentially to the sink closest to the assimilating leaf (Rawson and Hofstra, 1969; Cook and Evans, 1978). Based on this evidence, the following simple hypothesis is proposed: only the parent tiller supplies carbohydrates for the appearance of its daughter tiller, and the relative sink strength of the tiller bud (i.e. the sink strength of the tiller bud divided by the sum of the sink strengths on the parent tiller) is independent of temperature and light intensity. If so, a positive relation must exist between the dry matter increase of the parent tiller per phyllochron at the time of appearance of the daughter tiller and the specific site usage of that daughter tiller. In the current experiment root weight per tiller was not measured, but was calculated by assuming that each tiller type had a share in root weight proportional to its above-ground weight. Figure 8 shows that there is a positive relation between the specific site usage and the dry matter production (leaves, sheaths and roots) per phyllochron of the parent tiller. The relationship varied with tiller type: e.g. t0.0 appeared at a lower dry matter production per phyllochron of its parent tiller than the other tillers.

This mechanism of carbohydrate availability could explain differences in specific site usage between different light intensity and temperature conditions. Differences between

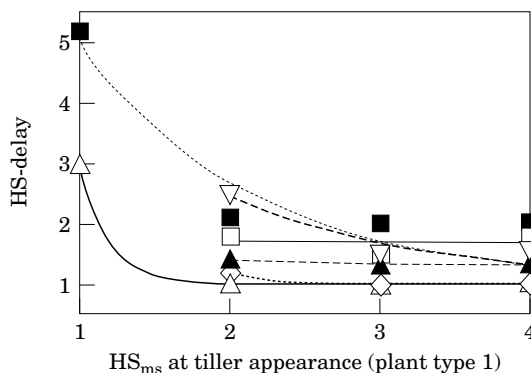


FIG. 9. Published values of HS-delay as a function of quantitative tiller parameter 'HS<sub>ms</sub> at tiller appearance (plant type 1)' for several Gramineae species: ■, winter wheat [Klepper *et al.*, 1982, their table 1 (field)]; □, winter wheat [Masle-Meynard and Sebillotte, 1981, their figure 1: pots treatment (growth chamber)]; ▲, winter wheat [Rickman *et al.*, 1985, their figure 5 (growth chamber)]; △, ryegrass [Mitchell, 1953, his figure 6, treatment S.R. 2000-50 (growth chamber)]; ▽, orchardgrass [Ito *et al.* (1987), their table 1 (growth chamber)]; ◇, tall fescue [Ito *et al.* (1987), their table 1 (growth chamber)]. Data were fitted with eqn. 6; each curve starts within the marker of the matching data set.

tiller types could occur owing to bud size: e.g. t0.0 buds are relatively small and need smaller amount of assimilates to grow out, as reflected in the small size of the first leaves of this tiller compared with other tillers (Bos and Neuteboom, 1998).

#### Regulation of HS-delay

The HS-delay of both spring and winter wheat depended mainly on the tiller timing parameter: 'HS<sub>ms</sub> calculated from plant type 1', and much less on tiller position parameters, light intensity or temperature. This implies that HS-delay does not depend primarily on specific effects of light or temperature, nor on assimilate availability of the whole plant or at the tillering site. Apparently, HS-delay is determined principally by stage of plant development.

Spring and winter wheat showed a large difference in HS-delay for equal tiller positions. Figure 9 shows values of HS-delay for primary tillers of grasses and cereals, which could be calculated from the literature. In two experiments, the HS-delay was as low as 1, for ryegrass (*Lolium* spp.) (Mitchell, 1953) and tall fescue (*Festuca arundinacea* Schreb.) (Ito *et al.*, 1987), indicating that variation in HS-delay among species of Gramineae is large.

Figures 6 and 9 show a clearly-decreasing HS-delay with plant development stage, which does not accord with the constant HS-delay often assumed (Davies, 1974; Masle-Meynard and Sebillotte, 1981; Neuteboom and Lantinga, 1989). Why tillers are delayed at an early plant development stage independent of environmental conditions is unknown. At later stages plants seem to reach a more constant HS-delay.

Light intensity showed little effect on HS-delay, as also shown by data for orchardgrass (*Dactylis glomerata* L.) and tall fescue (Ito *et al.*, 1987), and winter wheat for tiller t0 (Peterson, Klepper and Rickman, 1982); temperature had a small effect on HS-delay. Tillers with a specific site usage of

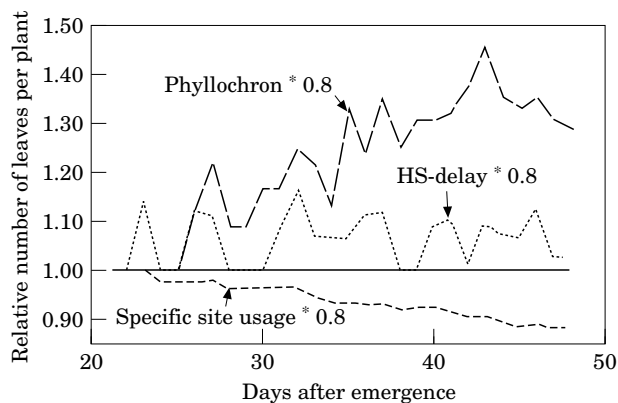


FIG. 10. Effect of a 20% reduction in phyllochron, HS-delay or specific site usage of each tiller on the number of leaves per plant relative to the original values for treatment TIL3. Day 21 (first harvest) was considered as starting point.

less than 1 showed a markedly higher HS-delay (Figs 5 and 6), indicating that the HS-delay increases with higher temperatures or lower light intensities only when conditions are only just satisfactory for tiller appearance.

#### Towards a dynamic mechanistic model

Phyllochron has been studied extensively, and existing models (e.g. Volk and Bugbee, 1991) can be used for simulation. In a dynamic model, the HS-delay can be seen as a 'window of opportunity', which opens after the parent tiller has reached a certain HS. Then the assimilate production of the parent tiller, the relative sink strength of the tiller bud, and the amount of assimilate needed to grow out into a visible tiller, determine whether the bud develops into a visible tiller (specific site usage). As can be seen in Fig. 10, phyllochron, HS-delay, and specific site usage have an important effect on leaf number per plant. This concept could be the basis for modelling leaf and tiller dynamics of Gramineae species in which effects of light intensity and temperature, and probably also other factors (CO<sub>2</sub>, plant density) could be included. We are currently developing such a model.

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