Journal of Agricultural Science (2005), **143**, 137–150. © 2005 *Cambridge University Press*
doi:10.1017/S0021859605005083 *Printed in the United Kingdom*

CENTENARY REVIEW

Phytomers, phyllochrons, phenology and temperate cereal development

G. S. McMASTER

2150 Centre Ave., Bldg D, Suite 200, Fort Collins, CO, 80526, USA

(*Revised MS received 16 September 2004*)

SUMMARY

Extensive research has been conducted on temperate cereal development since the inception of the *Journal of Agricultural Science, Cambridge* in 1905. This review presents an overview of the orderly and predictable development of wheat (*Triticum aestivum* L.) and barley (*Hordeum vulgare* L.). It begins with the concept of building canopies by the formation, growth and senescence of phytomers (the unit comprised of the leaf, axillary bud, node and internode). Morphological naming schemes for uniquely identifying each plant part are then extended to uniquely name each phytomer unit. The role of the phyllochron (rate of leaf appearance) in synchronizing cereal development and phytomer formation is discussed, as is the use of phenology to predict the timing of the formation, growth and senescence of individual components. The complete developmental sequence of the winter wheat shoot apex correlated with growth stages is extended to spring barley. This overview discusses the abiotic factors controlling cereal development, with special attention given to key questions regarding the critical role of temperature. The review concludes with some cautious glances forward to the exciting possibilities for better understanding of mechanisms controlling the phyllochron and phenology being gained from advances in functional genomics and molecular biology.

INTRODUCTION

> *The grasses are a vast group, and a correspondingly vast mass of information about them has been accumulated by botanists. If this information were brought together and correlated, it would form a library rather than a volume.*
>
> A. Arber (1934)

From earliest times, humans have gathered information on plants, albeit a somewhat informal form of documentation until the past few centuries. Interest has been great regarding the progression of plants though their life cycle and ultimately providing seeds, fruits, leaves, stems and tubers. In addition, knowledge of the stage at which plants should be harvested for medicinal value was of vital interest. These interests increased as groups moved from hunting and gathering societies to agrarian cultures. Grasses have played an increasingly important role in agriculture, and today are the dominant agricultural crops. Although Goethe first coined the term 'morphology' in the late eighteenth century, much of our scientific understanding of grasses has occurred since the later nineteenth century. Dissemination of knowledge was greatly expanded by the creation of agricultural journals; the *Journal of Agricultural Science, Cambridge* was one of the earliest when first published in 1905. As Agnes Arbor pointed out, by 1934 a vast accumulation of information about grasses had been accomplished. The state of knowledge in 1934 has been dwarfed by the exponential explosion of research in the latter half of the twentieth century, and one can only imagine what Agnes Arber would write today about our accumulated information. A significant focus of the work on grasses has been on the agriculturally significant temperate small-grain cereals, wheat (*Triticum aestivum* L.) and barley (*Hordeum vulgare* L.).

An extensive conceptual framework of cereal development has been devised, resulting in many tools for predicting cereal development with remarkable accuracy. The foundation of this work is that cereals develop in an orderly and predictable manner, especially when environmental conditions are not

Email: Greg.McMaster@ars.usda.gov

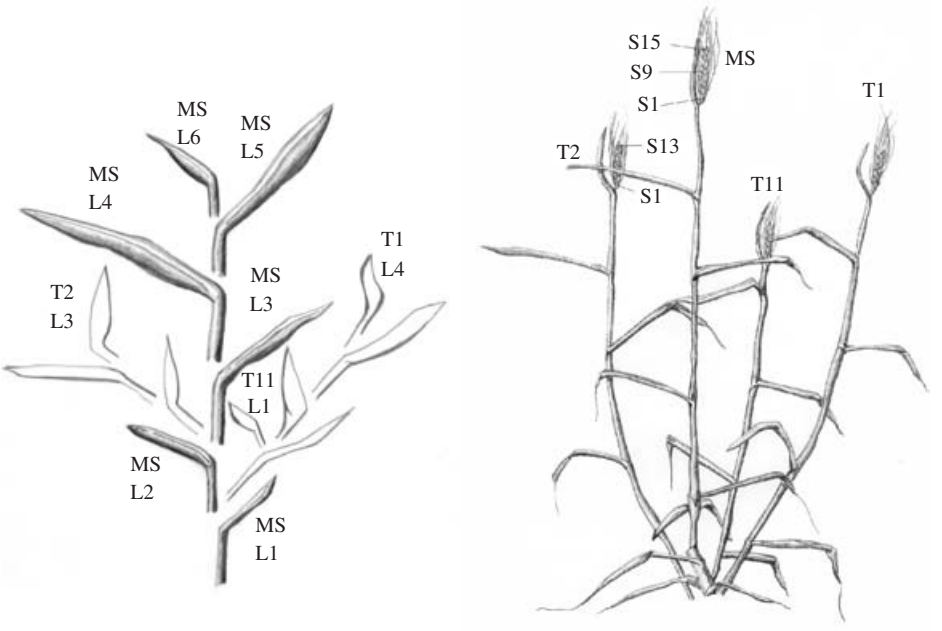

Fig. 1. Building plant canopies by the addition of phytomer units. Morphological naming schemes for vegetative tissues according to Klepper *et al.* (1983*a*) and reproductive tissue by Wilhelm & McMaster (1996). Adapted from McMaster (2002).

limiting. The pattern of development remains the same for different genotypes with variation mainly occurring in the rate or duration of specific developmental events, suggesting a strong genetic control. The pattern remains the same for varying environments, again with variation primarily in the rate or duration of specific developmental events within a genotype. Some genotypes and developmental events vary more than others to specific environmental stresses.

Centennial journal issues provide opportunities and incentives to consider the historical path leading to our current knowledge and where the path may lead in the future. Yet restraint is necessary, because temperate cereal development is too vast a subject to review in complete detail here, and readers are directed to more detailed reviews that offer varying perspectives (e.g. Engledow & Ramiah 1930; Evans & Grover 1940; Bonnett 1966; Milthorpe & Ivins 1966; Langer 1979; Kirby & Appleyard 1984; Hay & Kirby 1991; Rickman & Klepper 1995; McMaster 1997). A more modest goal is to present a general overview of selected key concepts of wheat and barley development that emerge from these reviews. Most concepts apply to other grasses, and often all plants, and are based on the premise that development is orderly and predictable. The fundamental purpose of this review is to describe how wheat and barley (and by inference, other grass) canopies are built by the formation, growth and senescence of phytomers. The role of the plastochron and phyllochron in coordinating the phytomers is combined with the vast work on phenology to predict the orderly development of cereals. The review finishes with a wary glance towards the future and possible role of functional genomics in better explaining the mechanisms controlling cereal development.

BUILDING CANOPIES

Just as anatomy often views the cell as the fundamental building block of tissues, the phytomer can be considered the fundamental building block of plant canopies. Plants construct their canopies by the repeated formation, expansion and senescence of a basic unit, the phytomer. The phytomer concept dates at least to Gray (1879), and the phytomer unit usually is defined as consisting of a leaf and the associated axillary bud, node and internode (Evans & Grover 1940). The phytomer unit originates at the shoot apex with the leaf initial. A shoot is constructed by the sequential addition of phytomer units at the shoot apex. Each component of the phytomer unit can continue to differentiate and grow, resulting in its visible appearance (Fig. 1). For instance, the leaf initial can continue to differentiate and grow, resulting in the appearance of the leaf blade from the subtending whorl of leaves. If the axillary bud differentiates and grows, then a tiller may appear from the axil of the leaf in the form of a leaf blade.

The associated internode may grow from cells derived from the intercalary meristem under certain conditions leading to the separation of the nodes of each phytomer on the shoot. At any stage (depending on environment and genetics) of differentiation and growth, a phytomer component may then begin to senesce. Generally, the leaf is the primary phytomer component that senesces, and towards the death of the shoot the internode tissue senesces. Each shoot is built in the same manner, and a field could be viewed as a population of phytomers forming, growing and senescencing.

One important consideration of this model is how the axillary bud differentiates and grows. In the model described in the previous paragraph for wheat and barley, the axillary bud forms a new shoot. In some annual grasses such as maize (*Zea mays* L.), the axillary bud can either develop into another shoot or a female inflorescence (e.g. the ear). Another variation of significance is whether the leaf initial continues to differentiate and grow. Once the shoot apex switches from vegetative to reproductive events at the time of single double ridge, leaf initials stop further development. At double ridge, the ridge formed above the leaf initial which develops into the spikelet could be viewed as the 'axillary bud'. One then could extend the phytomer unit concept in the developing spike as the leaf initial, the spikelet initial leading to the spikelet primordium, and the node and internode would ultimately be the node and internode on the rachis.

NAMING PLANT PARTS AND PHYTOMERS

Recognizing that canopies are built by phytomers necessitates that we be able to uniquely identify the phytomer units on each plant to allow precise communication when describing the processes. In order to develop a naming scheme for phytomers, we can build on existing morphological naming schemes for each part of the plant. Leaf morphological naming schemes are the cornerstone of identifying each plant tissue. Leaves are numbered acropetally on a shoot (Jewiss 1972; Klepper *et al.* 1982, 1983*a*), with the first true leaf designated L1, the second L2, and so on until the flag leaf (Fig. 1). Haun (1973) formally created a growth staging system that accounts for the total number of true leaves produced on a shoot:

$$\text{Haun stage} = (n-1) + L_n/L_{n-1}, \quad [0 \leqslant (L_n/L_{n-1}) \leqslant 1] \qquad (1)$$

where n is the number of leaves that have appeared on the shoot, L_{n-1} is the blade length of the penultimate leaf, and L_n is the blade length of the youngest expanding leaf that is visible emerging from the sheath of the penultimate leaf. An example would be if the third leaf blade on a shoot is emerging from the whorl of leaves and the blade length is half the blade length of the penultimate leaf, the Haun stage would be 2·5.

A variety of shoot naming schemes for annual grasses have been proposed (Katayama 1931; Jewiss 1972; Klepper *et al.* 1982, 1983*a*). In these naming schemes, the first culm to emerge from the seed is considered the main shoot (MS). Primary tillers are those derived from the axils of leaves on the main shoot, with a designation of T#, where # refers to leaf number of the main shoot. For instance, T1 is the primary tiller emerging from the axil of L1 on the MS (Fig. 1). Secondary tillers are those derived from primary tiller leaves and designated as T##, where the first # refers to the parent primary tiller number and the second # is the leaf number of the parent primary tiller that subtends the secondary tiller. An example would be the T11 tiller which emerges from the first leaf of the primary tiller T1 (Fig. 1). Similar designations are given for tertiary (e.g. T111) and higher order tillers. An anomalous tiller, the coleoptile tiller, is derived from the axil of the coleoptile leaf. This primary tiller is designated as TC by some (Kirby & Eisenberg 1966) and T0 by Klepper *et al.* (1982, 1983*a*).

Once the leaf on each shoot can be uniquely named, this naming scheme is easily adapted to nodes and internodes, where node number (and the internode above the node) is the same as the leaf number.

The leaf numbering system has been used to develop a nomenclature for cereal root systems (Klepper *et al.* 1984). Each root axis is designated with the associated number of the node and direction of orientation in respect to the associated leaf on each shoot. What is particularly intriguing is that wheat root axes are developed in a synchronized pattern based on shoot development related to leaf appearance.

Nomenclature for inflorescence tissue is needed to complete the morphological naming schemes for the entire plant. Within grasses, Allred (1982) and Allred & Columbus (1988) delineated grass inflorescence types and applied floral formulas. The naming conventions for leaves and tillers can easily be adapted to uniquely identify the wheat and barley spike. Numerical scales for reporting the progression of inflorescence development were created by Klepper *et al.* (1983*b*) and Sweet *et al.* (1991), in addition to more traditional growth stage scales discussed below. Wilhelm & McMaster (1996) further developed this earlier work into a scheme for uniquely naming each spikelet and floret/kernel within a spikelet on each shoot within a wheat and barley grass spike. As with leaves, each spikelet within the spike is numbered acropetally. To illustrate this, the first spikelet on the main stem is denoted as MS, S1 (Fig. 1). Each floret/caryopsis is numbered acropetally within a spikelet as well, with F/C used to denote the floret or caryopsis,

respectively (e.g. MS, S4, C1 would be the basal kernel in the fourth spikelet from the base of the main shoot spike). In cases such as six-rowed barley where multiple spikelets occur at each rachis node, the spikelets are further delineated with a lowercase letter (a, b, or c for six-rowed barley) arranged from left to right when viewed with the rachis behind the spikelets.

Although each leaf, node, internode, spikelet, floret, and caryopsis can be uniquely named, the naming schemes have not been extended to identifying the phytomer unit directly. Rickman & Klepper (1995) used the term phyllome to include the vegetative phytomer (i.e. plastochron), extended leaf blades (i.e. phyllochron), reproductive phytomer (i.e. spikelets), and florets, yet this only approached a naming scheme for phytomer units. The naming schemes for individual plant parts can easily be extended to naming the vegetative and reproductive phytomers of wheat and barley. As with leaves that are numbered acropetally on a shoot starting with L1, the first phytomer associated with the first leaf is denoted with a 'P' and would be P1. Because it is important to know that this phytomer is associated with a leaf that is growing beyond the leaf initial, the use of 'L' is added to the designation, giving PL1. The next phytomer would be PL2, etc. up to the flag leaf on the culm, which would be PL*n*, where *n* equals the leaf number. The culm designation can be added to identify which shoot is being discussed (e.g. MS, PL3 for the third phytomer on the main stem).

Once the single ridge stage is reached, the leaf initial does not further differentiate and grow, rather the spikelet initial does. These phytomer units can be identified by using the spikelet naming scheme beginning with the basal spikelet and numbering them acropetally and inserting a 'P' in front. For example, the basal spikelet 'phytomer' in the spike would be designated as PS1, and the terminal spikelet for wheat would be PS*n*. For two-rowed barley no modifications are necessary, but six-rowed barley would add the lowercase 'a', 'b', or 'c' discussed above to identify the specific spikelet at each position on the rachis (e.g. PSb1 would be the central spikelet in the basal spikelet position in six-rowed barley).

THE PHYLLOCHRON AND PLASTOCHRON

Because canopies are built by the formation, growth and senescence of phytomers, the timing of the formation at the shoot apex of the phytomers and subsequent growth and senescence of the phytomer components becomes of great interest. Phytomer formation is dependent on the initiation of leaf primoridia, and therefore the rate of primoridia initiation controls the timing of the phytomer formation. Much attention has focused on the rate of leaf primordium initiation and leaf appearance and many terms have been applied to these processes. Askenasy (1880, as cited by Erickson & Michelini 1957) first coined the term plastochron, and defined it as the interval between the formation of two successive internode cells. The term was expanded later by Milthorpe (1956) and Esau (1965) to include the interval between the initiation of successive primordia on the shoot apex. Further refinement of the concept and generation of new terms such as auxochron (Hancock & Barlow 1960) and phyllochron (Bunting & Drennan 1966) were proposed. Although confusion among these terms exists, general usage today uses the plastochron for the rate of primordium initiation and the phyllochron for the rate of leaf appearance (Wilhelm & McMaster 1995).

Depending on the species, the relationship of the plastochron to the phyllochron varies. For rice (*Oryza sativa* L.), the plastochron rate and phyllochron rate is the same (about a 1:1 ratio), while for wheat and barley the ratio is about 2:1 where leaf primordia are produced more quickly than they appear (Baker & Gallagher 1983; Kiniry *et al.* 1991). The initiation of reproductive phytomers (i.e. spikelet initials) tends to be about 3–4 times faster than vegetative phytomers (i.e. leaf initials, Rickman & Klepper 1995; McMaster 1997). Regardless of the ratio, both the plastochron and phyllochron are quite predictable based on temperature, with other abiotic factors having secondary effects and often only after a threshold value is reached. In addition, the plastochron and phyllochron vary among genotypes (Frank & Bauer 1995) and planting dates within a year (Baker *et al.* 1980; Porter *et al.* 1987).

Unfortunately, while many data sets exist that measure the phyllochron, efforts to create equations to accurately predict the phyllochron have not been very successful. Several analyses (Bindi *et al.* 1995; Kirby 1995; McMaster & Wilhelm 1995) have tested at least nine different equations for different cultivars, locations and environments and none was suitably robust. The 'best' equations used the change of day length at the time of seedling emergence based largely on the earlier work of Baker *et al.* (1980) and Porter *et al.* (1987). While a satisfactory correlation can be found using this relationship, it suffers from a lack of understanding of the underlying mechanisms controlling the phyllochron. To date, no satisfactory equation has been developed.

The phyllochron is also a useful predictor for the time at which the axillary bud begins differentiation and growth leading to a new shoot. Each tiller has a window of time when the axillary bud can begin differentiation and growth, and once this window passes the axillary bud normally does not initiate further growth (Klepper *et al.* 1982). The timing of this window is correlated with leaf appearance (Klepper *et al.* 1982). The end result is that phytomers appear on

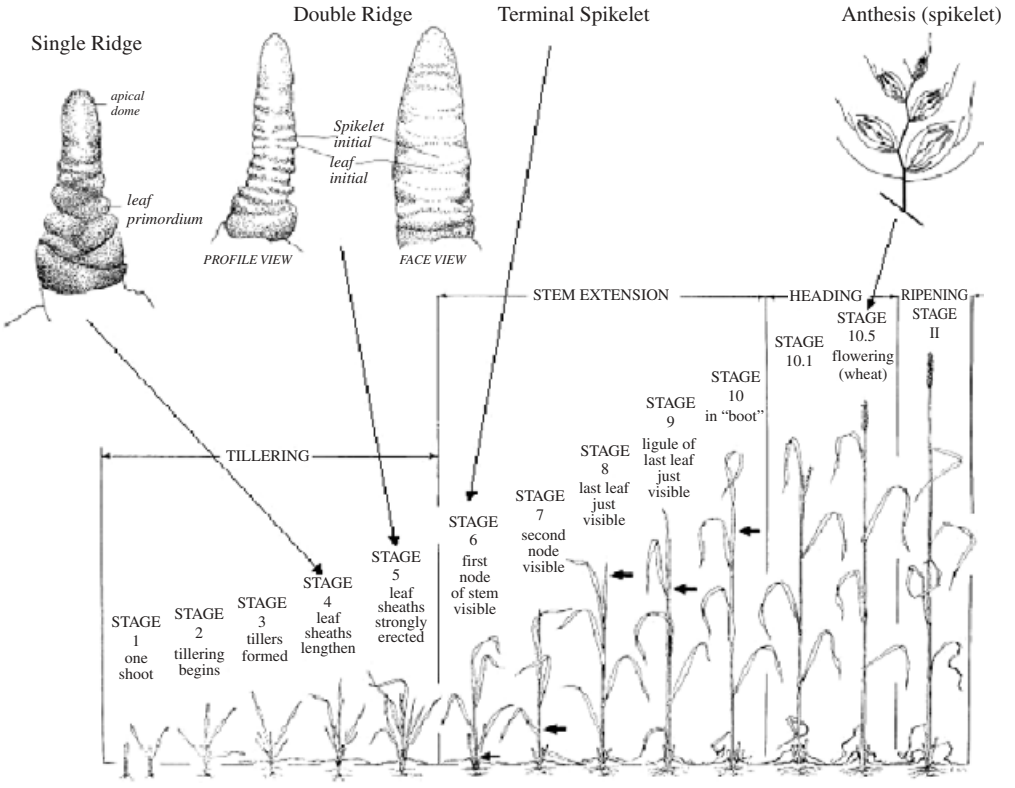

Fig. 2. The Feekes Growth Stage Scale (Large 1954) correlated with the approximate timing of certain shoot apex growth stages.

culms and new shoots appear in plants in an orderly and predictable pattern based on the phyllochron and leaf number. Hay & Kirby (1991) discuss the synchrony of shoots within a plant to reach maturity at nearly the same time.

PHENOLOGY

While the population dynamics of phytomers can describe the pattern of construction of cereal canopies, it does not tell us when the switch from vegetative to reproductive phytomers occurs or when specific phytomer components such as internodes begin to elongate. The well-studied and often reviewed timing of growth stages, or phenology, can be used to predict these events. A wide variety of growth stage scales have been available for quite some time (e.g. Large 1954; Jeater 1956; Haun 1973; Zadoks *et al*. 1974). Earlier scales such as Feekes (Fig. 2; Large 1954) focused on stages of caryopsis maturation, but later scales have included increasingly greater attention to both vegetative stages and stages only visible by dissection of the plant and examination of the shoot apex (Fig. 2). While many similarities exist among growth scales, increasing efforts have been made to create a unified growth staging system both for cereals and for all crops (Lancashire *et al*. 1991). Converting among scales is sometimes difficult, and guides (Bauer *et al*. 1983) and computer programs (Harrell *et al*. 1993, 1998) are available for assistance. Use of growth stage scales is so widespread and provides such an important context for many plant measurements that journals now often require some indication of the growth stages during which measurements were taken (Frank *et al*. 1997).

SYNTHESIS OF THE DEVELOPMENTAL SEQUENCE

Based on extensive earlier work, formal syntheses of shoot apex and canopy development in various forms were created at the end of the twentieth century. Prior to 1990, various excellent summaries of the developmental sequence existed, but these focused on portions of the developmental sequence, did not always correlate various shoot apex developmental events with phenological growth stages, and tended to be qualitative.

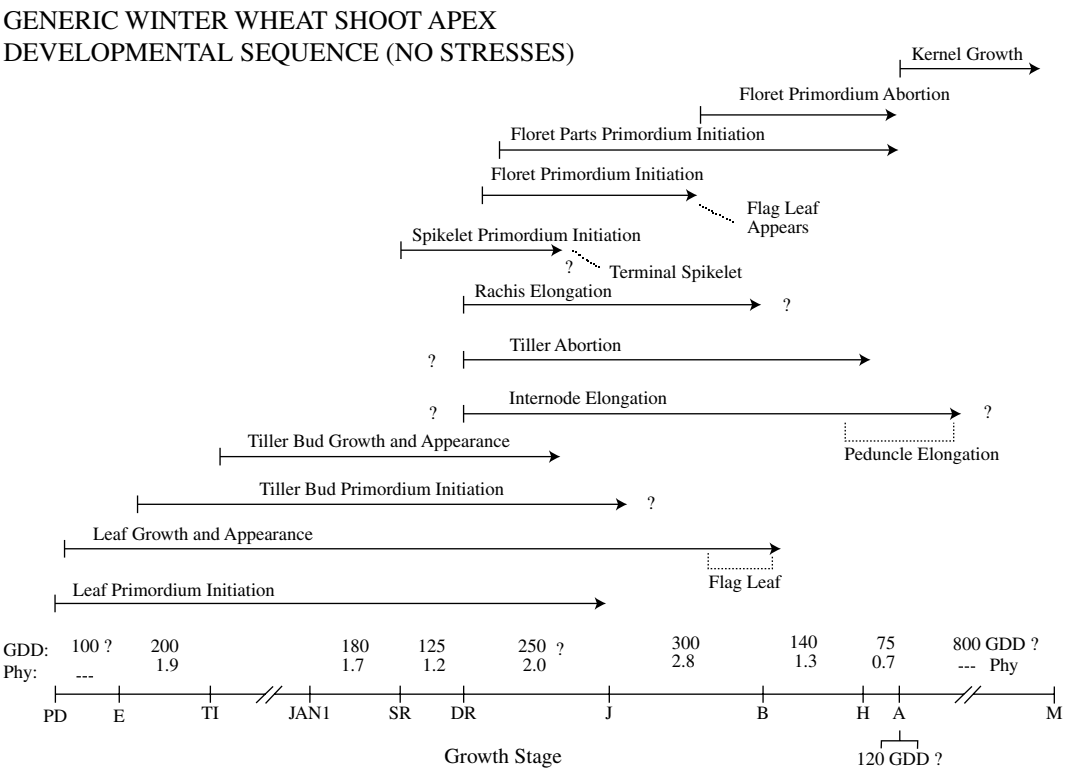

Fig. 3. Developmental sequence of the generic winter wheat shoot apex for optimal conditions. Question marks refer to uncertainty, important cultivar variation, or conflicting reports in the literature. Time line legend is: GDD, accumulated growing degree-days for the interval; Phy, number of phyllochrons for the interval; PD, planting date; E, seedling emergence; TI, tiller initiation/appearance; SR, single ridge; DR, double ridge; J, jointing; B, booting; H, heading; A, anthesis; and M, physiological maturity. Adapted from McMaster *et al.* (1992*b*).

Rickman & Klepper (1995) elegantly presented the most complete template relating the coordinated appearance of each phytomer unit to other developmental events such as single and double ridge for cereal crops. Depending on the species, rates varied but the general patterns were similar. Since quantifying this template for specific species was not the objective, appropriate parameters to quantify rates and timing of specific phenological events was usually not provided for either species or genotype.

A different synthesis published several years earlier (McMaster *et al.* 1992*a*, *b*) was not as explicitly based on the phytomer unit. This synthesis presented the complete sequence of when shoot apex processes such as leaf, tiller, spikelet, and floret primordia formed, grew, and senesced, and correlated these processes with the timing of phenological growth stages for a generic winter wheat plant (Fig. 3). Quantification by either number of phyllochrons or thermal time is presented for each growth stage interval.

The complete developmental sequence published for a generic winter wheat plant provides a template for other cereal species due to the similarity in development as discussed earlier. Unpublished work in the mid-1990s, mainly from W. W. Wilhelm, A. B. Frank, B. Klepper and R. W. Rickman, altered the winter wheat template to a spring barley cultivar that normally produced seven leaves on the main stem (Fig. 4). Essentially all developmental events are the same between winter wheat and spring barley, with the exception that barley does not have a true terminal spikelet as in wheat because it is an indeterminate inflorescence. The presence of the development of awn initials signals the equivalent of a terminal spikelet because spikelets formed after this do not further differentiate and grow. Extrapolations from winter wheat to winter barley and spring barley to spring wheat are easily made as primarily only the thermal time between phenological events changes, mainly due to differences in the phyllochron.

Aspects of these syntheses have been captured to varying degrees in developmentally based simulation models such as ARCWHEAT (Weir *et al.* 1984), MODWht (Rickman *et al.* 1996), WHTROOT

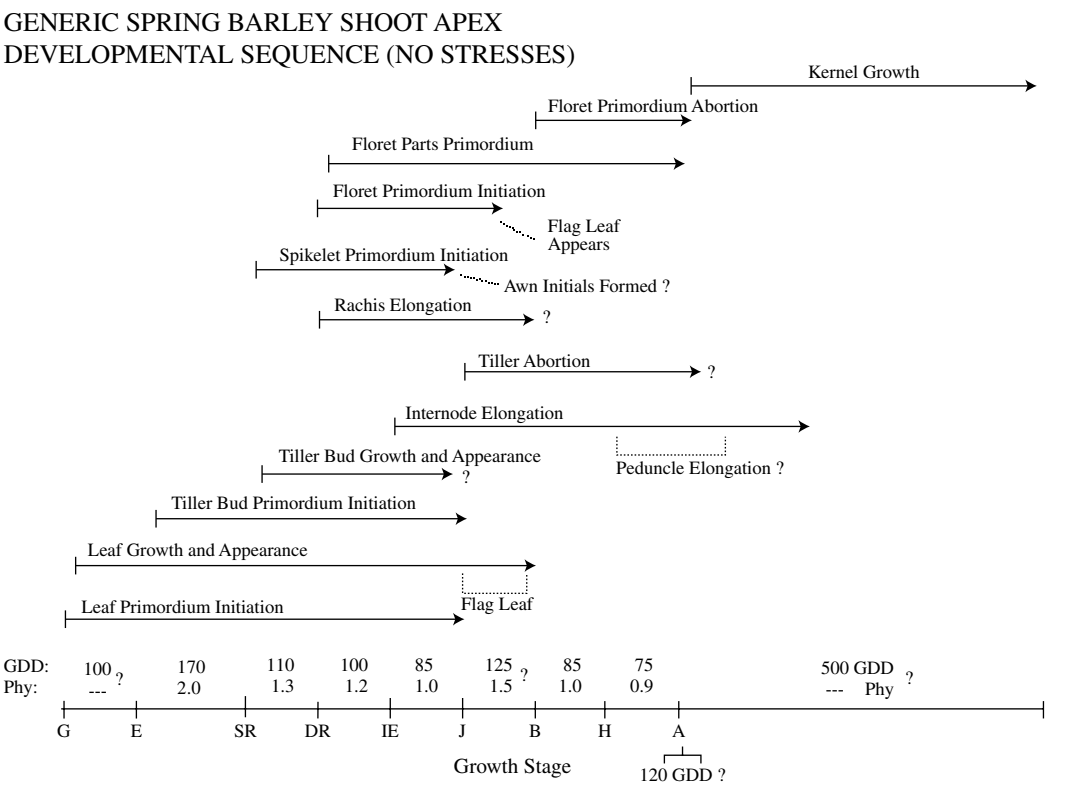

Fig. 4. Developmental sequence of the generic 7-leaved spring barley shoot apex for optimal conditions. Question marks refer to uncertainty, important cultivar variation, or conflicting reports in the literature. See Fig. 3 for time line legend. This diagram is based on unpublished work with W. W. Wilhelm, A. Frank, B. Klepper and R. W. Rickman.

(Porter *et al*. 1986), and SHOOTGRO (McMaster *et al*. 1991, 1992*a*, *b*; Wilhelm *et al*. 1993; Zalud *et al*. 2003). While the MODWht and SHOOTGRO models capture the processes outlined in Figs 3 and 4, a generic phytomer model for annual grasses could be built using the template provided by Rickman & Klepper (1995) and taking other information from the MODWht and SHOOTGRO models to generate a generic developmentally based grass model.

TEMPERATURE AND TEMPERATE CEREAL DEVELOPMENT

Many environmental factors interact with the genetics to influence the phyllochron and phenological development. While no single environmental factor completely predicts development, temperature and occasionally photoperiod are clearly the most critical factors (Baker & Gallagher 1983; Hunt & Chapleau 1986; Kirby & Perry 1987; Cao & Moss 1989*a*, *b*; Masle *et al*. 1989). Water availability can also affect phenology (McMaster 1997), although the effect on the phyllochron seems considerably less pronounced (Baker *et al*. 1986; Maas & Grieve 1990). McMaster & Wilhelm (2003) found that water availability reduced the thermal time required to reach later growth stages the most, particularly shortening grain-filling duration by about 20 %. Because growth stages prior to flag leaf appearance were not affected by water availability, this supports the use of the phyllochron interval for predicting earlier growth stages and partly explains the poorer correlation with later growth stages, especially in a crop such as wheat that is frequently grown in extremely water-limited conditions. Other abiotic factors such as nutrients, CO_2 and some aspects of light can alter the phyllochron and phenology, but are of secondary importance to temperature and normally require a certain threshold level be reached before having an effect (Boone *et al*. 1990; Longnecker *et al*. 1993; McMaster *et al*. 1999). Where abiotic factors such as water, nutrients, CO_2, salinity, and light do play a critical role is on the growth and senescence of the components of the phytomer. For instance, water, N and carbohydrate availability (as influenced by CO_2 and light) all influence cell expansion leading to growth. This is

manifested in numerous examples such as whether axillary buds further differentiate and grow resulting in tiller appearance, final leaf size and morphology, leaf senescence rates and tiller abortion.

The importance of temperature in plant growth has been recognized for many centuries and there have probably been many efforts to quantify temperature. The second century Greek physician and philosopher Galen suggested that reference points for a temperature scale could be ice and boiling water (Windelspecht 2002). However, few further efforts in developing instruments to measure temperature can be found until Galileo published a primitive thermometer in 1610. (A significant drawback to Galileo's design was the impact of barometric pressure on the liquid of choice, wine.) Shortly after this, one of the first known uses of a thermometer in scientific research was by Sanctorius in experiments in human physiology and temperature. In 1641, Ferdinando de' Medici substantially improved the design of the thermometer and it has changed little since. Gabriel Fahrenheit and Anders Celsium developed the Fahrenheit and Celcius scales, respectively, in the early eighteenth century. Aside from academic historical interest, the key of this development was an easily measured, and most significantly, repeatable, means of quantifying temperature. However, a significant advancement in terms of understanding and predicting crop development was the concept of thermal time. Until this concept was advanced, calendar time was used. Clearly calendar time was a problem because warmer or cooler than normal seasons or years deviated from the expected development rate or stage.

Wang (1960) attributes the origin of the thermal time concept to Rene Reaumur around 1735. Although using a temperature scale not in use today, Reaumur developed a thermal constant of phenology expressing the amount of heat required for a plant to reach a specific stage of maturity. As the concept matured, the canonical form of Eqn 2 is the basis for calculating thermal time as represented for small grains in the commonly used growing degree-days (GDD) form:

$$\mathrm{GDD} = \sum ((T_{\max} + T_{\min})/2) - T_{\mathrm{base}}, \quad [\text{and } \mathrm{GDD} \geqslant 0] \qquad (2)$$

where $T_{\max}$ and $T_{\min}$ are the daily maximum and minimum temperature, T_{base} is the base temperature below which temperature has no effect (i.e. the process cannot occur), and the quantity is summed over an interval of days. The problem is that this equation has been interpreted in different ways resulting in differences of over 20% in the estimation of the GDD for a growing season using the same weather data, and it often is unclear how the equation is being interpreted (McMaster & Wilhelm 1997). Some confusion is associated with traditional interpretations of the equation which is dependent on the crop studied (i.e. small grains *v.* maize).

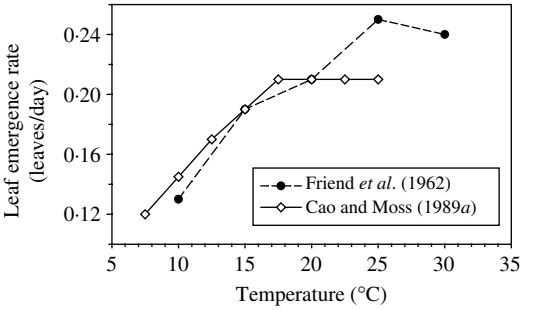

Fig. 5. Leaf emergence rates as a function of constant temperature. Leaf emergence rates are approximations from graphs presented in Friend *et al.* (1962) and Cao & Moss (1989*a*).

Numerous variations and attempts to refine Eqn 2 have been proposed. Occasionally upper threshold values have been included, some authors change the base temperature and upper threshold over the life cycle. Attempts have been made to integrate daily temperature accumulation using shorter time intervals such as hourly or shorter time steps, and attempts have also been made to refine the relationship around various cardinal points including an estimate of optimum temperature to weight temperature (McMaster & Smika 1988; Yan & Hunt 1999; Streck *et al.* 2003). Although these modifications can slightly improve the calculation of GDD in certain instances, it seems that the simplest approach of Eqn 2 (using a constant 0 °C for Tbase; Baker & Gallagher 1983; McMaster & Smika 1988) is very robust and often sufficient for most purposes. Many databases have been created to estimate the GDD for various growth stages (with Nuttonson 1955 providing a very thorough early review) and phyllochron values for different wheat and barley genotypes.

Field experiments have often shown a linear relationship of growing degree-days to either the phyllochron or phenology in the field. This observation has clashed with growth chamber and greenhouse experiments, showing that the temperature response is not linear (Peacock 1975; Hay & Delecolle 1989; Slafer & Rawson 1997; Van Esbroeck *et al.* 1997). Approximating values for leaf emergence rates for different constant temperatures from Cao & Moss (1989*a*) and Friend *et al.* (1962), Fig. 5 shows this non-linear relationship with temperature, particularly for higher temperatures. Of note, however, is that for a range of temperatures of about 7–18 °C for eight winter wheat and barley varieties (Cao & Moss 1989*a*) or 10–25 °C for a spring wheat 'Marquis' (Friend *et al.* 1962), the relationship is approximately

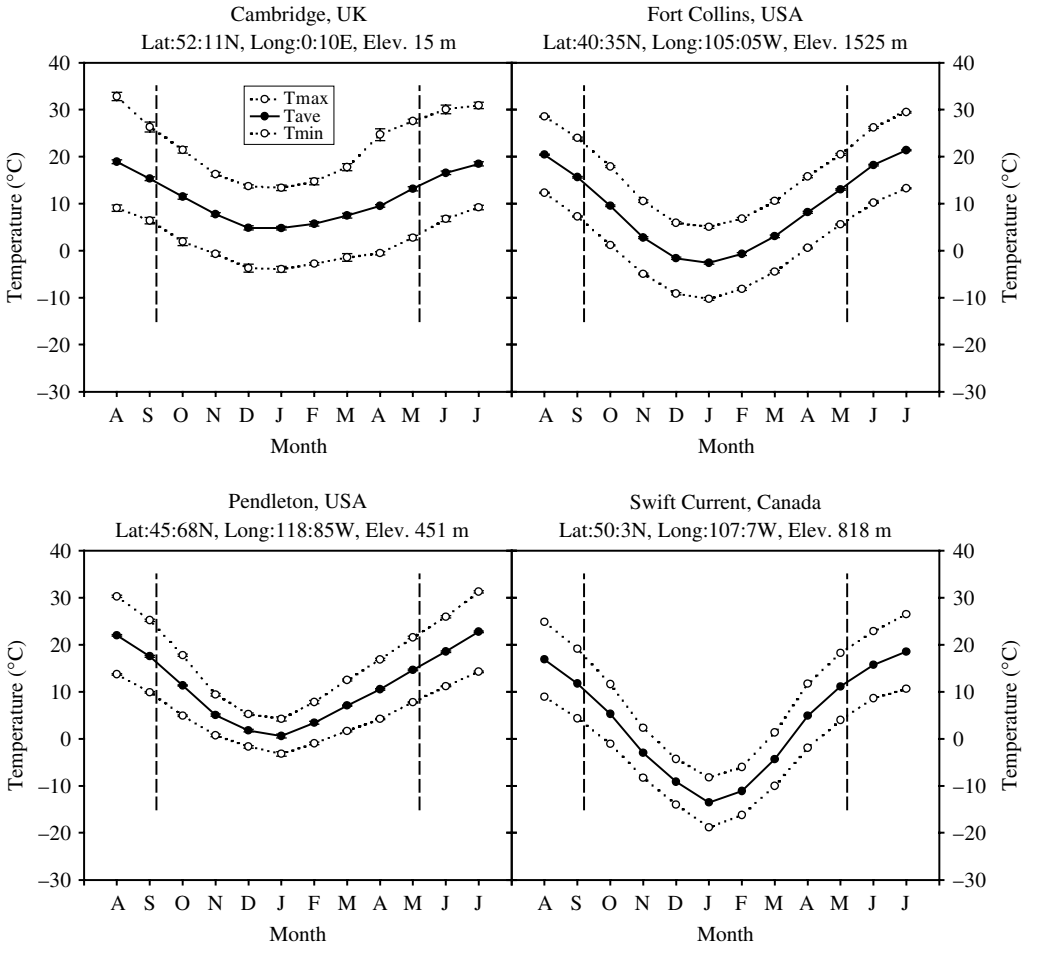

Fig. 6. Long-term monthly maximum, minimum, and average temperature data for four locations. The approximate period of leaf appearance is noted by dashed vertical lines.

linear. Extending the work of McMaster & Hunt (2003), the issue is resolved by examining temperature data. When long-term weather records for four locations are examined for the period when leaves are typically produced based on common planting dates (Fig. 6), it can be seen that monthly temperatures (particularly daily average temperatures) are within the linear portion of the temperature response curves shown in Fig. 5. The known non-linear temperature response in controlled conditions is further obscured by diurnal and daily temperature fluctuations lessening the impact of short periods of time when temperatures are outside of the linear phase.

Discussions of whether the phyllochron and phenology were linearly related to GDD also focused attention on where temperature should be measured. Most efforts used readily available and measured air temperature above the canopy to approximate shoot apex temperature. Yet, theory suggested a better approximation of shoot apex temperature would be achieved by using soil temperature. Theoretical considerations included that many developmental processes occur at the shoot apex (e.g. leaf primordia formation, single and double ridge) and the shoot apex perceives temperature (Peacock 1975). Since the shoot apex is located in the crown until internode elongation begins just prior to the growth stage of jointing, soil temperature at crown depth (about 20 mm below the soil surface) might better reflect apex temperature than air temperature above the canopy (Jamieson *et al.* 1995; Vinocur & Ritchie 2001). Experimental support came from a long history of root/shoot temperature experiments in growth chambers and some field experiments where temperature was altered by mulches or heating and corresponding changes in the phyllochron or phenology

were observed (Peacock 1975; Hay & Wilson 1982; Bollero *et al.* 1996; Stone *et al.* 1999). Unfortunately, although the reasoning and experimental data seemed to overwhelmingly support this hypothesis, troubling anomalies were noticed. McMaster & Wilhelm (1998) reported that using soil temperature did not improve phenological predictions over using air temperature for 21 site-years in the Central Great Plains of the US, and cited unpublished data by Klepper and Rickman for the Pacific Northwest of the US supporting this finding. However, none of these experiments directly tested the hypothesis that shoot apex temperature was the critical location. Therefore, an experiment was conducted in 1998 and 1999 for three planting dates of a spring wheat cultivar (Nordic). In each planting date, heating tape directly under the seed was used to elevate shoot apex temperature by 3 °C over ambient soil temperature at this depth. Unexpectedly, elevating the temperature at the seed/crown only shortened the duration of germination and seedling emergence and had no effect on either the phyllochron (McMaster *et al.* 2003*b*) or phenological development (McMaster & Wilhelm 2003). Because the discrepancies could not be explained, the following extensions to the existing paradigm were proposed, based on an integrated systems viewpoint. First, there are usually several active shoot apices within a plant, and rather than viewing each apex as independently forming, growing and senescing leaves controlled by the environment (particularly temperature), the apices and leaf life cycle should be viewed as coordinated processes (Hay & Kemp 1990). Certainly signalling from throughout the plant can affect individual shoot apex functioning. Second, the phyllochron can be divided into three processes: (a) cell division at the shoot apex forming the leaf initial; (b) cell division of the intercalary meristem of the expanding leaf primordium; and (c) growth of cells formed by the intercalary meristem resulting in leaf emergence. Temperature influences all three processes, but to varying degrees. Cell cycling time is strongly dependent on temperature, but cell growth is much more influenced by other factors such as carbohydrate, water and nutrient availability. Environmental conditions at other locations in the plant affect the availability of these resources, and thus shoot apex functioning and ultimately the phyllochron. Support for this reasoning is that the plastochron is more strongly related to temperature (essentially only cell division) than the phyllochron (which includes cell growth). Finally, recognition of where the processes are occurring vertically in space needs to be expanded. Rather than viewing the shoot apex as a point in space, even the relatively short shoot apex can be almost 10 mm in length (Kirby & Appleyard 1984). What had been ignored in the earlier paradigm was the intercalary meristem. The leaf extension zone can cover a vertical distance up to 70 mm (Skinner & Nelson 1995), and this could put at least some of the leaf extension zone above the soil surface.

PUTTING IT TOGETHER

The wheat and barley canopy is built by the addition of phytomers primarily characterized either by the leaf or spikelet component. Regardless, the plastochron determines the rate of formation, and can be readily approximated using thermal time as calculated by growing degree-days accumulated above the canopy with a 0 °C base temperature. Phenological modelling (also using growing degree-days, and possibly modified by photoperiod and vernalization responses not discussed), can predict when certain important developmental events occur, which can then be used to adjust the development, growth and senescence of individual phytomer components. For instance, internodes do not elongate until just prior to the growth stage of jointing. The first internode to begin elongating is in the youngest forming phytomer on the culm. Another example is that only leaf primordia formed before single ridge growth stage will continue to differentiate and appear at the rate of the phyllochron, which is also quantified using growing degree-days. Phenological models can also be used to predict other important canopy growth stages such as anthesis and physiological maturity. This sequence is repeated for each tiller on the plant, and the window of appearance of tillers is based on the leaf number (therefore the phyllochron) of the parent shoot.

This general template of cereal development provides the foundation of form that can then be integrated with function, or other areas of physiology. It allows an accurate depiction of all sources and sinks on the plant at any point in time, and morphological naming schemes allow unique identification of them. While this review has provided little discussion on the growth or senescence of phytomer components, much work has been done in this area. For instance, normally leaf size increases acropetally on a culm (Hay & Wilson 1982), and under unstressed conditions leaves begin to senesce about 6·5 phyllochrons after formation (McMaster *et al.* 1991).

MECHANISMS CONTROLLING CEREAL DEVELOPMENT AND THE FUTURE

Clearly, there is an orderly and predictable sequence of cereal development. It is also equally clear that the mechanisms underlying these processes are not well understood and are quite empirical. This review has ignored several problems with developing robust cereal development models, particularly how to move from the gene to the phenotype (Edmeades *et al.*

2004) and the ever-present dilemma of genotype by environment interaction (McMaster *et al*. 2003*a*; Baenziger *et al*. 2004). Interestingly, the inaugural issue of the *Journal of Agricultural Science, Cambridge* in 1905 may have given us a glimpse into the future of cereal development research: three papers addressed the recent rediscovery of Mendelian genetics (Biffen 1905*a*, *b*; Butler 1905). Although a great distance lay between this work and mapping of the *Arabidopsis thaliana* (L.) Heynh. genome in 2000 (Arabidopsis Genome Initiative 2000) and rice genome in 2003 (Bevan 2003), the path was set for better understanding of the mechanisms controlling cereal development. The explosion of information being generated from genomics and molecular biology research is beginning to provide some insight into the genetic controls on developmental processes.

Some of the biggest gains coming from functional genomics relevant to cereal development is found in the area of phenology, and particularly controls on the timing of flowering (Laurie 1997; Kato *et al*. 1999; Iwaki *et al*. 2002; Danyluk *et al*. 2003; Trevaskis *et al*. 2003; Yan *et al*. 2003, 2004; Nakagawa *et al*. 2005). A variety of photoperiod, cold hardiness and semidwarfing genes have also been identified and a great deal of knowledge is accumulating regarding these genes. Much has been learned from Arabidopsis and rice, but temperate cereals have diverged in some areas. An elegant conceptual model of the genetic controls for time of flowering of temperate cereals is summarized by Laurie *et al*. (2004), although the model is certain to be further refined as work continues.

Considerably less knowledge is available on genetic mechanisms controlling the phyllochron. Miyamoto *et al*. (2004) has identified QTLs for both the phyllochron and tillering in rice. However, it is likely that the genetic controls are quite complicated and this is merely the starting point for better understanding. The lack of understanding of the mechanisms controlling the phyllochron is reflected in our poor ability to predict the phyllochron in the equations developed to date. With the phyllochron so important in predicting cereal development, there is great need for further work in this area.

Some intriguing pioneering efforts to build on the accumulating genetic information is being used to model cold tolerance (Fowler *et al*. 1999), flowering time in Arabidopsis (Welch *et al*. 2003), and general crop growth (Hoogenboom & White 2003). Hunt *et al*. (2003) bring a needed degree of cautionary restraint on these modelling efforts by discussing many of the difficulties that are involved in such efforts, including epistatic and pleiotropic gene effects.

Physiology will also play a key role in future research. Not only is physiology needed to turn the genetic 'noise' into information, but the developmental sequences still have many areas of uncertainty and variability that need to be explained. The role of abiotic factors other than temperature, and how management practices alter the abiotic factors, needs greater exploration to further improve the efficacy of management practices. Nevertheless, we can apply our extensive existing knowledge to aid in the timing of management practices and address emerging issues such as cereal responses to possible changes in climate. Much has been learned since the inaugural issue in 1905 and Agnes Arber's quote from 1934.

Reviews such as this depend on the many scientists who have done the difficult work developing the concepts of cereal development. Selecting from the rich literature of their impressive work inevitably does injustice to the totality of their work and ideas. Unintentional biases on my part influenced the selection of work and ideas and possibly created a revisionist history – for which I apologize to any whom I have offended. I also appreciate the opportunity presented by R. E. L. Naylor to review their work. I learned much in the process.

REFERENCES

Allred, K. W. (1982). Describing the grass inflorescence. *Journal of Range Management* **35**, 672–675.

Allred, K. W. & Columbus, J. T. (1988). The grass spikelet formula: an aid in teaching and identification. *Journal of Range Management* **41**, 350–351.

Arabidopsis Genome Initiative (2000). Analysis of the genome sequence of the flowering plant *Arabidopsis thaliana*. *Nature* **408**, 796–815.

Arber, A. (1934). *The Gramineae: a Study of Cereal, Bamboo, and Grass*. Cambridge, UK: Cambridge University Press.

Askenasy, E. (1880). Über eine neue Methode, um die Vertheilung der Wachsthumsintintensität in wachsenden Theilen zu bestimmen. Verhandlungen. *Naturhistorisch-Medizinischer Verein zu Heidelberg* **2**, 70–153.

Baenziger, P. S., McMaster, G. S., Wilhelm, W. W., Weiss, A. & Hays, C. J. (2004). Putting genes into genetic coefficients. *Field Crops Research* **90**, 133–143.

Baker, C. K. & Gallagher, J. N. (1983). The development of winter wheat in the field. 2. The control of primordium initiation rate by temperature and photoperiod. *Journal of Agricultural Science, Cambridge* **101**, 337–344.

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

Baker, J. T., Pinter, P. J., Jr., Reginato, R. J. & Kanemasu, E. T. (1986). Effects of temperature on leaf appearance in spring and winter wheat cultivars. *Agronomy Journal* **78**, 605–613.

Bauer, A., Smika, D. & Black, A. (1983). *Correlation of Five Wheat Growth Stage Scales used in the Great Plains*. USDA ATT-NC-7. Peoria, ILL: Agricultural Research Service, U.S. Department of Agriculture.

Bevan, M. (2003). Surprises inside a green grass genome. *Science* **300**, 1514–1515.

Biffen, R. H. (1905*a*). Mendel's Laws of inheritance and wheat breeding. *Journal of Agricultural Science, Cambridge* **1**, 4–48.

Biffen, R. H. (1905*b*). The inheritance of sterility in the barleys. *Journal of Agricultural Science, Cambridge* **1**, 250–257.

Bindi, M., Porter, J. R. & Miglietta, F. (1995). Comparison of models to calculate leaf appearance in wheat. *European Journal of Agronomy* **4**, 15–26.

Bollero, G. A., Bullock, D. G. & Hollinger, S. E. (1996). Soil temperature and planting date effects on corn yield, leaf area, and plant development. *Agronomy Journal* **88**, 385–390.

Bonnett, O. T. (1966). *Inflorescences of Maize, Wheat, Rye, Barley and Oats: Their Initiation and Development*. University of Illinois College of Agriculture, Agricultural Experiment Station, Bulletin 721.

Boone, M. Y. L., Rickman, R. W. & Whisler, F. D. (1990). Leaf appearance rates of two winter wheat cultivars under high carbon dioxide conditions. *Agronomy Journal* **82**, 718–724.

Bunting, A. H. & Drennan, D. S. H. (1966). Some aspects of the morphology and physiology of cereal in the vegetative phase. In *The Growth of Cereal and Grasses*. Proc. 12th Easter School in Agricultural Science, Univ. of Nottingham, Nottingham, England (Eds F. L. Milthorpe & J. D. Ivins), pp. 20–38. London: Butterworths.

Butler, E. J. (1905). The bearing of Mendelism on the susceptibility of wheat to rust. *Journal of Agricultural Science, Cambridge* **1**, 361–363.

Cao, W. & Moss, D. N. (1989*a*). Temperature effect on leaf emergence and phyllochron in wheat and barley. *Crop Science* **29**, 1018–1021.

Cao, W. & Moss, D. N. (1989*b*). Daylength effect on leaf emergence and phyllochron in wheat and barley. *Crop Science* **29**, 1021–1025.

Danyluk, J., Kane, N. A., Breton, G., Limin, A. E., Fowler, D. B. & Sarhan, F. (2003). TaVRT-1, a putative transcription factor associated with vegetative to reproductive transition in cereals. *Plant Physiology* **132**, 1849–1860.

Edmeades, G. O., McMaster, G. S., White, J. W. & Campos, H. (2004). Genomics and the physiologist: bridging the gap between genes and crop response. *Field Crops Research* **90**, 5–18.

Engledow, F. L. & Ramiah, K. (1930). Investigations on yield in cereals. VII. A study of development and yield of wheat based upon varietal comparison. *Journal of Agricultural Science, Cambridge* **20**, 265–347.

Erickson, R. O. & Michelini, F. J. (1957). The plastochron index. *American Journal of Botany* **44**, 297–305.

Esau, K. (1965). *Plant Anatomy*. New York: John Wiley & Sons, Inc.

Evans, M. W. & Grover, F. O. (1940). Developmental morphology of the growing point of the shoot and the inflorescence in grasses. *Journal of Agricultural Research* **61**, 481–520.

Fowler, D. B., Limin, A. E. & Ritchie, J. T. (1999). Low-temperature tolerance in cereals: model and genetic interpretation. *Crop Science* **39**, 626–633.

Frank, A. B. & Bauer, A. (1995). Phyllochron differences in wheat, barley, and forage grasses. *Crop Science* **35**, 19–23.

Frank, A. B., Cardwell, V. B., Ciha, A. J. & Wilhelm, W. W. (1997). Growth staging in research and crop management. *Crop Science* **37**, 1039–1040.

Friend, D. J. C., Helson, V. A. & Fisher, J. E. (1962). Leaf growth in Marquis wheat, as regulated by temperature, light intensity, and daylength. *Canadian Journal of Botany* **40**, 1299–1311.

Gray, A. (1879). *Structural Botany*. New York: Ivsion, Blakeman, Taylor, and Company.

Hancock, C. R. & Barlow, H. W. B. (1960). Short-term fluctuations in leaf and internode growth in the apple root stock crab C. *New Phytologist* **59**, 227–237.

Harrell, D. M., Wilhelm, W. W. & McMaster, G. S. (1993). SCALES: A computer program to convert among three developmental stage scales for wheat. *Agronomy Journal* **85**, 758–763.

Harrell, D. M., Wilhelm, W. W. & McMaster, G. S. (1998). Scales 2: Computer program to convert among developmental stage scales for corn and small grains. *Agronomy Journal* **90**, 235–238.

Haun, J. R. (1973). Visual quantification of wheat development. *Agronomy Journal* **65**, 116–119.

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**, 333–341.

Hay, R. K. M. & Kemp, D. R. (1990). Primordium initiation at the stem apex as the primary event controlling plant development: preliminary evidence from wheat for the regulation of leaf development. *Plant Cell and Environment* **13**, 1005–1008.

Hay, R. K. M. & Kirby, E. J. M. (1991). Convergence and synchrony – a review of the coordination of development in wheat. *Australian Journal of Agricultural Research* **42**, 661–700.

Hay, R. K. M. & Wilson, G. T. (1982). Leaf appearance and extension in field-grown winter wheat plants: the importance of soil temperature during vegetative growth. *Journal of Agricultural Science, Cambridge* **99**, 403–410.

Hoogenboom, G. & White, J. W. (2003). Improving physiological assumptions of simulation models by using gene-based approaches. *Agronomy Journal* **95**, 82–89.

Hunt, L. A. & Chapleau, A.-M. (1986). Primordia and leaf production in winter wheat, triticale, and rye under field conditions. *Canadian Journal of Botany* **64**, 1972–1976.

Hunt, L. A., Reynolds, M. P., Sayre, K. D., Rajaram, S., White, J. W. & Yan, W. (2003). Crop modeling and the identification of stable coefficients that may reflect significant groups of genes. *Agronomy Journal* **95**, 20–31.

Iwaki, K., Nishida, J., Yanagisawa, T., Yoshida, H. & Kato, K. (2002). Genetic analysis of VRNk-B1 for vernalization requirement by using linked dCAPS markers in bread wheat (*Triticum aestivum* L.). *Theoretical and Applied Genetics* **104**, 571–576.

Jamieson, P. D., Brooking, I. R., Porter, J. R. & Wilson, D. R. (1995). Prediction of leaf appearance in wheat: a question of temperature. *Field Crops Research* **41**, 35–44.

Jeater, R. S. L. (1956). A method for determining developmental stages in grasses. *Journal of British Grassland Society* **27**, 139–146.

Jewiss, O. R. (1972). Tillering in grasses – its significance and control. *Journal of the British Grassland Society* **27**, 65–82.

Katayama, T. (1931). Analytical studies of tillering in paddy rice. *Journal of the Imperial Agricultural Experiment Station, Japan* **1**, 327–374.

Kato, K., Miura, H. & Sawada, S. (1999). QTL mapping of genes controlling ear emergence time and plant height on chromosome 5A of wheat. *Theoretical and Applied Genetics* **98**, 472–477.

Kiniry, J. R., Rosenthal, W. D., Jackson, B. S. & Hoogenboom, G. (1991). Predicting leaf development of crop plants. In *Predicting Crop Phenology* (Ed. T. Hodges), pp. 29–42. Boca Raton, FL: CRC Press.

Kirby, E. J. M. (1995). Factors affecting rate of leaf emergence in barley and wheat. *Crop Science* **35**, 11–19.

Kirby, E. J. M. & Appleyard, M. (1984). *Cereal Development Guide*. Second edition. Coventry, UK: Arable Unit, National Agricultural Centre.

Kirby, E. J. M. & Eisenberg, B. E. (1966). Some effects of photoperiod on barley. *Journal of Experimental Botany* **17**, 204–213.

Kirby, E. J. M. & Perry, M. W. (1987). Leaf emergence rates of wheat in a Mediterranean environment. *Australian Journal of Agricultural Research* **38**, 455–464.

Klepper, B., Rickman, R. W. & Peterson, C. M. (1982). Quantitative characterization of vegetative development in small cereal grains. *Agronomy Journal* **74**, 789–792.

Klepper, B., Rickman, R. W. & Belford, R. K. (1983*a*). Leaf and tiller identification on wheat plants. *Crop Science* **23**, 1002–1004.

Klepper, B., Tucker, T. W. & Dunbar, B. D. (1983*b*). A numerical index to assess early inflorescence development in wheat. *Crop Science* **23**, 206–208.

Klepper, B., Belford, R. K. & Rickman, R. W. (1984). Root and shoot development in winter wheat. *Agronomy Journal* **76**, 117–122.

Lancashire, P. D., Bleiholder, H., Van Den Boom, T., Langeluddeke, P., Strauss, R., Weber, E. & Witzenberger, A. (1991). A uniform decimal code for growth stages of crops and weeds. *Annals of Applied Biology* **119**, 561–601.

Langer, R. H. M. (1979). *How Grasses Grow*. Institute of Biology Studies Series. London: Edward Arnold.

Large, E. C. (1954). Growth stages in cereals. *Plant Pathology* **3**, 128–129.

Laurie, D. A. (1997). Comparative genetics of flowering time. *Plant Molecular Biology* **35**, 167–177.

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**, 87–100.

Longnecker, N., Kirby, E. J. M. & Robson, A. (1993). Leaf emergence, tiller growth, and apical development of nitrogen-deficient spring wheat. *Crop Science* **33**, 154–160.

Maas, E. V. & Grieve, C. M. (1990). Spike and leaf development in salt-stressed wheat. *Crop Science* **30**, 1309–1313.

Masle, J., Doussinault, G., Farquhar, G. D. & Sun, B. (1989). Foliar stage in wheat correlates better to photothermal time than to thermal time. *Plant, Cell and Environment* **12**, 235–247.

McMaster, G. S. (1997). Phenology, development, and growth of the wheat (*Triticum aestivum* L.) shoot apex: a review. *Advances in Agronomy* **59**, 63–118.

McMaster, G. S. (2002). Modeling field crop and rangeland canopy development, structure, and dynamics. *Acta Horticulturae* **593**, 165–170.

McMaster, G. S. & Hunt, L. A. (2003). Re-examining current questions of wheat leaf appearance of temperature. In *Modeling Temperature Response in Wheat and Maize. Proceedings of a workshop, CIMMYT, El Batan, Mexico, 23–25 April 2001, Natural Resources Group, Geographic Information Systems Series 0301* (Ed. J. W. White), pp. 18–22. Mexico: CIMMYT.

McMaster, G. S. & Smika, D. E. (1988). Estimation and evaluation of winter wheat phenology in the central Great Plains. *Agricultural and Forest Meteorology* **43**, 1–18.

McMaster, G. S. & Wilhelm, W. W. (1995). Accuracy of equations predicting the phyllochron of wheat. *Crop Science* **35**, 30–36.

McMaster, G. S. & Wilhelm, W. W. (1997). Growing degree-days: one equation, two interpretations. *Agricultural and Forest Meteorology* **87**, 291–300.

McMaster, G. S. & Wilhelm, W. W. (1998). Is soil temperature better than air temperature for predicting winter wheat phenology? *Agronomy Journal* **90**, 602–607.

McMaster, G. S. & Wilhelm, W. W. (2003). Phenological responses of wheat and barley to water and temperature: improving simulation models. *Journal of Agricultural Science, Cambridge* **141**, 129–147.

McMaster, G. S., Klepper, B., Rickman, R. W., Wilhelm, W. W. & Willis, W. O. (1991). Simulation of shoot vegetative development and growth of unstressed winter wheat. *Ecological Modelling* **53**, 189–204.

McMaster, G. S., Morgan, J. A. & Wilhelm, W. W. (1992*a*). Simulating winter wheat spike development and growth. *Agricultural and Forest Meteorology* **60**, 193–220.

McMaster, G. S., Wilhelm, W. W. & Morgan, J. A. (1992*b*). Simulating winter wheat shoot apex phenology. *Journal of Agricultural Science, Cambridge* **119**, 1–12.

McMaster, G. S., Lecain, D. R., Morgan, J. A., Aiguo, L. & Hendrix, D. L. (1999). Elevated CO_2 increases CER, leaf and tiller development, and shoot and root growth. *Journal of Agronomy and Crop Science* **183**, 119–128.

McMaster, G. S., Ascough Ii, J. C., Shaffer, M. J., Deer-Ascough, L. A., Byrne, P. F., Nielsen, D. C., Haley, S. D., Andales, A. A. & Dunn, G. H. (2003*a*). GPFARM plant model parameters: complications of varieties and the genotype X environment interaction in wheat. *Transactions of the American Society of Agricultural Engineers* **46**, 1337–1346.

McMaster, G. S., Wilhelm, W. W., Palic, D. B., Porter, J. R. & Jamieson, P. D. (2003*b*). Spring wheat leaf appearance and temperature: extending the paradigm. *Annals of Botany* **91**, 697–705.

Milthorpe, F. L. (1956). The relative importance of the different stages of leaf growth in determining the resultant area. In *The Growth of Leaves*. Proc. 3rd Easter School in Agricultural Science, Univ. of Nottingham, Nottingham,

England (Ed. F. L. Milthorpe), pp. 20–38. London: Butterworths.

Milthorpe, F. L. & Ivins, J. D. (Eds.). (1966). *The Growth of Cereals and Grasses*. Proceedings of the Twelfth Easter School in Agricultural Science, University of Nottingham, 1965. London: Butterworths.

Miyamoto, N., Goto, Y., Matsui, M., Ukai, Y., Morita, M. & Nemoto, K. (2004). Quantitative trait loci for phyllochron and tillering in rice. *Theoretical and Applied Genetics* **109**, 700–706.

Nakagawa, H., Yamagishi, J., Miyamoto, N., Motoyama, M., Yano, M. & Nemoto, K. (2005). Flowering response of rice to photoperiod and temperature: a QTL analysis using a phenological model. *Theoretical and Applied Genetics* **110**, 778–786.

Nuttonson, M. Y. (1955). *Wheat-climate Relationships and the use of Phenology in Ascertaining the Thermal and Photo-thermal Requirements of Wheat*. Washington, DC: American Institute of Crop Ecology.

Peacock, J. M. (1975). Temperature and leaf growth in *Lolium perenne*. II. The site of temperature perception. *Journal of Applied Ecology* **12**, 115–123.

Porter, J. R., Klepper, B. & Belford, R. K. (1986). A model (WHTROOT) which synchronizes root growth and development with shoot development for winter wheat. *Plant and Soil* **92**, 133–145.

Porter, J. R., Kirby, E. J. M., Day, W., Adam, J. S., Appleyard, M., Ayling, S., Baker, C. K., Beale, P., Belford, R. K., Biscoe, P. V., Chapman, A., Fuller, M. P., Hampson, J., Hay, R. K. M., Hough, M. N., Matthews, S., Thompson, W. J., Weir, A. H., Willington, V. B. A. & Wood, D. W. (1987). An analysis of morphological development stages in Avalon winter wheat crops with different sowing dates and at ten sites in England and Scotland. *Journal of Agricultural Science, Cambridge* **109**, 107–121.

Rickman, R. W. & Klepper, E. L. (1995). The phyllochron: Where do we go in the future? *Crop Science* **35**, 44–49.

Rickman, R. W., Waldman, S. E. & Klepper, B. (1996). MODWht3: A development-driven wheat growth simulation. *Agronomy Journal* **88**, 176–185.

Skinner, R. H. & Nelson, C. J. (1995). Elongation of the grass leaf and its relationship to the phyllochron. *Crop Science* **35**, 4–10.

Slafer, G. A. & Rawson, H. M. (1997). Phyllochron in wheat as affected by photoperiod under two temperature regimes. *Australian Journal of Plant Physiology* **24**, 151–158.

Stone, P. J., Sorensen, I. B. & Jamieson, P. D. (1999). Effect of soil temperature on phenology, canopy development and yield of cool-temperate maize. *Field Crops Research* **63**, 169–178.

Streck, N. A., Weiss, A., Xue, Q. & Baenzinger, P. S. (2003). Improving predictions of developmental stages in winter wheat: a modified Wang and Engel model. *Agricultural and Forest Meteorology* **115**, 139–150.

Sweet, N., Wiltshire, J. J. J. & Baker, C. K. (1991). A new descriptive scale for early reproductive development in *Lolium perenne* L. *Grass and Forage Science* **46**, 201–206.

Trevaskis, B., Bagnall, D. J., Ellis, M. H., Peacock, W. J. & Dennis, E. S. (2003). MADS box genes control vernalization-induced flowering in cereals. *Proceedings of the National Academy of Science USA* **100**, 13099–13104.

Van Esbroeck, G. A., Hussey, M. A. & Sanderson, M. A. (1997). Leaf appearance rate and final leaf number of switchgrass cultivars. *Crop Science* **37**, 864–870.

Vinocur, M. G. & Ritchie, J. T. (2001). Maize leaf development biases caused by air-apex temperature differences. *Agronomy Journal* **93**, 767–772.

Wang, J. Y. (1960). A critique of the heat unit approach to plant response studies. *Ecology* **41**, 785–790.

Weir, A. H., Bragg, P. L., Porter, J. R. & Rayner, J. H. (1984). A winter wheat crop simulation model without water or nutrient limitations. *Journal of Agricultural Science, Cambridge* **102**, 371–382.

Welch, S. M., Roe, J. L. & Dong, Z. (2003). A genetic neural network model of flowering time control in *Arabidopsis thaliana*. *Agronomy Journal* **95**, 71–81.

Windelspecht, M. (2002). *Groundbreaking Scientific Experiments, Inventions and Discoveries of the 17th Century*. Westport, Connecticut: Greenwood Press.

Wilhelm, W. W. & McMaster, G. S. (1995). The importance of the phyllochron in studying the development of grasses. *Crop Science* **35**, 1–3.

Wilhelm, W. W. & McMaster, G. S. (1996). Spikelet and floret naming scheme for grasses with a spike inflorescence. *Crop Science* **36**, 1071–1073.

Wilhelm, W. W., McMaster, G. S., Rickman, R. W. & Klepper, B. (1993). Aboveground vegetative development and growth of winter wheat as influenced by nitrogen and water availability. *Ecological Modelling* **68**, 183–203.

Yan, L., Loukoianov, A., Blechl, A., Tranquilli, G., Ramakrishna, W., Sanmiguel, P., Bennetzen, J. L., Echenique, V. & Dubcovsky, J. (2004). The Wheat VRN2 gene is a flowering repressor down-regulated by vernalization. *Science* **303**, 1640–1644.

Yan, L., Loukoianov, A., Tranquilli, G., Helguera, M., Fahima, T. & Dubcovsky, J. (2003). Positional cloning of the wheat vernalization gene VRN1. *Proceedings of the National Academy of Science USA* **100**, 6263–6268.

Yan, W. & Hunt, L. A. (1999). An equation for modelling the temperature response of plants using only the cardinal temperatures. *Annals of Botany* **84**, 607–614.

Zadoks, J. C., Chang, T. T. & Konzak, C. F. (1974). A decimal code for the growth stages of cereals. *Weed Research* **14**, 415–421.

Zalud, Z., McMaster, G. S. & Wilhelm, W. W. (2003). Evaluating SHOOTGRO 4.0 as a potential winter wheat management tool in the Czech Republic. *European Journal of Agronomy* **19**, 495–507.