The Phyllochron: Where Do We Go in the Future?

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ABSTRACT

This paper integrates, expands, and applies information from seven articles written for a symposium on the use of phyllochron concepts for describing shoot development in grasses. Generally, no one environmental factor is a perfect predictor of plant development rate. Factors that influence development rate include genetics, nutrition, water supply, day length, light, and temperature. Average air temperature, when accumulated in the form of a degree-day sum, does at times correlate linearly with plant developmental descriptors such as the Haun stage. The interval between visual appearance of successive leaves (the phyllochron) may be approximated as a constant number of degree-days for such a situation. If not only the visual extension of plant organs but the initiation of both vegetative and reproductive organs at active growing points can be linearly correlated with average temperature sums, an elegantly simple line diagram illustrates the full season synchronous initiation and development of all plant vegetative and reproductive parts. Development of each organ at the cellular level may be represented. This simple but complete representation of synchronous development based on the phyllochron provides a foundation for describing and improving understanding of the genetic and environmental control of grass development rate.

PLANT SHOOTS develop by forming, in sequence at each axis meristem, a series of nearly identical building blocks, called phytomers. The appearance or extension rate of each new phytomer is often irregular on a calendar scale but has, in many instances, been nearly constant when timed with thermal units. This simple relationship, when reliable, provides an easy method for predicting crop development as an aid for precision crop management in both commercial and research situations. The use of the phyllochron – the time interval between appearance of successive leaves – as a constant interval to describe and time plant development has greatly advanced our understanding and ability to anticipate organ by organ development of plants. In all too many instances, however, an irregular or nonlinear relationship between phytomer formation or extension and thermal units confounds attempts to precisely predict development. The insight into plant development provided by the use of the phyllochron as a developmental timing unit certainly justifies both the continuing search for a method to describe it as a constant value and for a method to predict that value from site to site and year to year.

This symposium was to examine current understanding of the timing of development of plant phytomers in cereal or perennial forage grass plants. Grass development may be described at several levels of detail ranging from the cell division that creates a new phytomer in an axis apex to extension of mature visible leaf blades of successive phytomers. Individual papers in this symposium have provided detail on several of these levels of description. The purpose of this paper is to integrate and apply the information in these individual papers and to point out directions for future research.

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VIEWPOINTS PRESENTED IN SYMPOSIUM

Wilhelm and McMaster (1995) defined terminology so that we may exchange concepts with a common understanding of the words used to describe the timing of grass development. Four primary terms provide the basis of our attempts to produce a quantitative description of plant development: phytomer (the node, internode, leaf, root buds, and tiller bud unit that is the vegetative building block of the plant), plastochron (the time interval between formation of successive phytomers at the growing point), phyllochron (the time interval between visual appearance of the tips of extending leaf blades of successive phytomers), and plant leaf (usually refers to just the leaf blade). These terms will be used to illustrate the interwoven synchrony of development of successive plant phytomers.

Kirby (1995) documented our frustration with current measures of developmental time. The term *developmental time* in some quantifiable interval will arise repeatedly in this paper and will hopefully be clarified with each revisitation. For now, consider the interval of plant developmental time to be the phyllochron, expressed in units of degree-days for conversion to calendar time and measured by observing blade extension of the leaves from successive phytomers.

The plant does not develop in proportion to time as measured on the human calendar. Instead, it responds to a thermal measure of time such as degree-days. Even then, there are secondary environmental factors that cause plant development rate to deviate from a constant value with respect to degree-days. Day length, seedbed temperature, soil water and fertility supply, and other conditions may moderate development rate. Even in fortunate situations or when using complex thermal or photothermal scales, the length of the interval of plant developmental time differs from time to time and place to place.

The most consistent correlation between observed length of the developmental time unit (phyllochron) in thermal time (degree-days) is with rate of change of day length (Baker et al., 1980). The correlation often provides the correct direction of change in length of the phyllochron with different planting dates, but the magnitude may be under or overestimated by 25% or more.

Kirby (1995) suggested that we may have to consider shifting the base temperature of our degree-day computations depending on soil temperatures during emergence if we are to obtain a developmental time unit of constant interval. This shift would imply that the base temperature of a particular crop is not totally determined genetically. Environmental factors (among them seed bed temperature during emergence) may modify the base temperature

appropriate for degree-day computations from one site or season to another.

McMaster and Wilhelm (1995) reinforced the frustration of Kirby (1995) with our lack of ability to predict the development interval for cereal plants (primarily wheat) in diverse environments. There appears to be a notable difference in our ability to predict phyllochrons for spring and winter wheat types. Variables that correlate with the phyllochron interval for spring wheat do not for winter wheat. Why should winter and spring wheat types differ in the way rate of development responds to environment?

Frank and Bauer (1995) provided examples of both genetic and environmental control of the interval of developmental time. For both forage grasses and cereal crops other than rice, there is relatively little information available on the possible range of phyllochron interval and genetic sources that may control it. Breeders consistently will select for early or late maturing cultivars, but the phyllochron time interval is rarely a conscious variable of the selection.

Nemoto et al. (1995) presented an overview of the remarkable depth of the Japanese literature on rice development. Phytomer development is synchronous at both initiation and at leaf blade emergence. In other words, the plastochron and the phyllochron are equal for rice. There are five stages of development of the rice phytomer ranging from cell division at the growing point to cell maturity with leaf blade extension. Each is one phyllochron (or plastochron) in length, and during vegetative growth, there will be one and only one phytomer in each of the four immature stages at all times. Detailed descriptions of the development of the rice phytomer have been extended to include the formation of not only the tiller bud, but the formation of multiple root buds and their associated branching for each phytomer. Internode elongation and development of reproductive phytomers have also been described in exquisite detail for rice. The recent English translation of Japanese literature on rice development and growth (Matsuo and Hoshikawa, 1993) is a stunning revelation of the depth and extent of existing knowledge of rice development and growth.

Skinner and Nelson (1995) described development of the phytomer at the cellular level in tall fescue (*Festuca arundinacea* Schreber). Each phytomer begins with cell division at a growing point. Cells comprising the phytomer elongate, differentiate, and mature to form the extended leaf blade, sheath, node, internode, roots, and a branch or tiller bud. Cells of successive phytomers repeat the same division–elongation–maturation sequence with a uniform offset in developmental time between successive phytomers.

Moore and Moser (1995) pointed out that the developmental indexes used on annual cereals did not provide information needed for forage grass management. They illustrated the need for describing greater diversity of developmental stage among existing culms in forage grasses and the need to describe coexisting vegetative and reproductive culms that do not normally occur in annual cereal crops. The Nebraska growth staging system is used for forage grasses.

INTEGRATION OF SYMPOSIUM INFORMATION

Diagrams used in this paper to illustrate the internal synchrony of successive plant phytomers have been constructed using six simplifying assumptions for unstressed plants. First and foremost is the assumption that plants have a developmental timing interval that is constant. We use the phyllochron for that interval. Cumulative growing degree-days with a base temperature appropriate for temperate or tropical crops (0°C for wheat, 12°C for rice) provide a first approximation for a constant measure of this interval. The physical observation of the phyllochron interval begins with the appearance of one leaf tip and ends with the appearance of the tip of the succeeding leaf. For grasses, the Haun developmental stage (Haun, 1973) is convenient for recording vegetative development and determining the phyllochron interval. There are observed cases of linear correlation of cumulative growing degree-days and Haun development stage for the complete growing season (Belford et al., 1987; Rickman et al., 1985). There also are cases where the observed relationship is bilinear or nonlinear (Hay and Delécolle, 1989; Baker et al., 1986; Cao and Moss, 1991). Perhaps these nonlinear cases will be explained as our knowledge expands.

A second assumption is that there is a simple relationship between the rate of phytomer initiation (the plastochron) and the rate of leaf development as determined by leaf blade extension (the phyllochron). There is usually either a 2:1 or 1:1 ratio between the interval of the phyllochron and that of the plastochron (Kiniry et al., 1991). Third, the time between initiation of successive reproductive phytomers (spikelets in wheat) is assumed to be one-quarter the interval of the phyllochron. Fourth, these intervals do not change during any one growing season, although they may differ from one planting date to another within a season or from one growing season to another. Fifth, once internode extension begins, successive internodes extend in intervals equal in time to those of the leaves (the phyllochron). Sixth, successive florets form at the interval of the plastochron. This is a rather restrictive set of assumptions, any one of which has observed examples of noncompliance. In spite of that fact, the framework of developmental timing and synchronization of phytomer development at the cellular and leaf appearance level that these assumptions together project is surprisingly close to most observations available for comparison.

The concepts based on the above assumptions are presented in Fig. 1 as the cornerstone for analysis of synchronous development within the plant. The vertical axis labeled *number of phyllomes* provides the scale for counting four different things: vegetative phytomers, extended leaf blades, spikelets, and florets. Each is counted from 0 to some value according to the length of the line segment that illustrates the time and rate of appearance of that particular part of the plant. The horizontal axis is cumulative degree-days from planting. These degree-day numbers provide the exact timing of all events illustrated in Fig. 1.

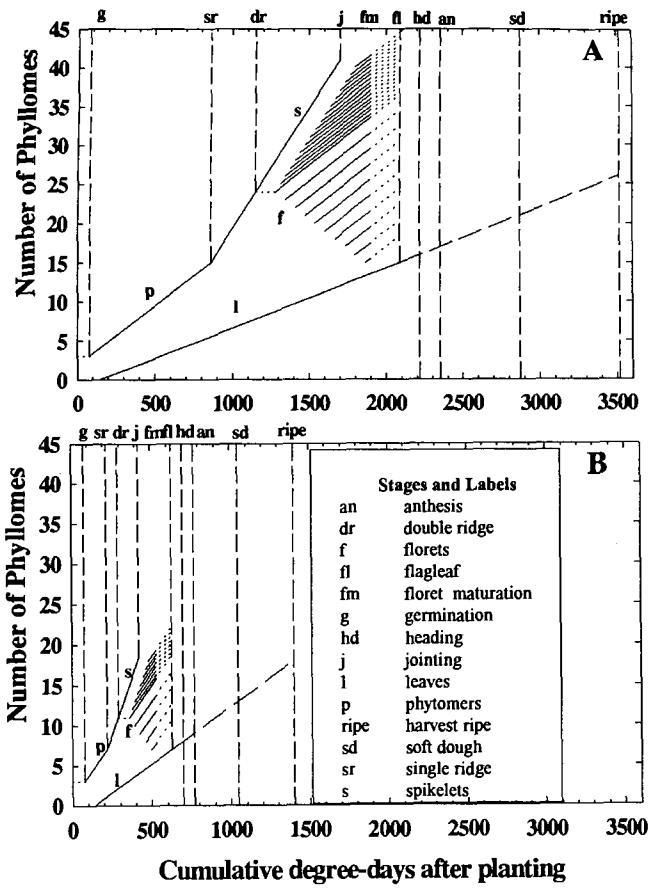

Fig. 1. Phyllome formation: phytomer and spikelet component appearance patterns for wheat with (A) a phyllochron interval of 130 degree-days and Leaf Number 15 as flag leaf and (B) a phyllochron interval of 70 degree-days and Leaf Number 7 as flag leaf. Crop development stages are shown where they occur.

First of the things counted by the y-axis scale is the number of phytomers initiated at the growing point. They are represented by the straight line segment labeled p in Fig. 1. The slope of Line Segment p represents the rate of formation in units of phytomers per degree-day. The inverse of this slope is the interval of the plastochron in degree-days per phytomer. Second, the number (as represented by Haun stage) and time of appearance of extended leaf blades are shown by the line segment labeled l. The inverse of the slope of Line Segment l is the interval of the plastochron. Phyllome numbers larger than the number of the flag leaf are the spikelet positions of the wheat spike. The number of spikelets and their time of formation are represented by the solid line segment labeled s. It extends upward and to the right from the upper end of Segment p. The phyllome number that is one larger than the number of the flag leaf is Spikelet Number one. These three line segments (p, phytomers; l, leaves; s, spikelets) have been used previously to illustrate relative rates of phytomer initiation, leaf extension, and spikelet formation. (Kirby, 1990). Along Line Segment s, horizontal lines can be extended from each spikelet position. Movement to the right along these horizontal lines represents the progressive development of the corresponding spikelet as timed by the degree-days of the x-axis. One of these horizontal lines is drawn in Fig. 1a and b. It is the dotted line at Spikelet Position 9 (Phyllome 24) in Fig. 1a, or the dotted line at Spikelet Position 4 (Phyllome 11) in Fig. 1b. When a spikelet is one phyllochron old, it begins to produce florets. The number of florets on the spikelet is represented by a solid line segment that begins one phyllochron after the spikelet was formed and extends upward and to the right at the rate of two florets per phyllochron. The vertical axis phyllome scale applies except that each floret count starts at zero where its line segment begins. The multiple solid line segments parallel to this line represent the formation of florets at each corresponding spikelet. The count for each, of course, starts at zero at the beginning of each segment. Each of these parallel lines ends as a dotted line that extends to the time of flag leaf extension. Florets formed and visible, as represented by the dotted portion of each line, do not survive to produce kernels.

The time of reproductive stage transitions are shown along the top of the figure. The position of each of these stages is located at the time (accumulated degree-days of the x-axis) of occurrence of corresponding developmental events as predicted by the linear developmental assumptions that created the figure and the reasoning explained below. These stage transitions do not occur at fixed degree-day sums (compare Fig. 1a and b for example) but occur as the plant develops, as controlled by its developmental timing rates and built in synchrony diagrammed in Fig. 1.

The number of spikelets that form on a spike can be estimated before they form if the time of occurrence of both single ridge and jointing can be determined. A three-phyllochron interval for the elongation of three internodes between jointing and flag leaf fully extended can be used to determine the time of jointing relative to flag leaf extension. The development stage of jointing and formation of terminal spikelet of the wheat spike occur in concert with one another (Hay and Kirby, 1991). The end result of this round-about logic is once flag leaf number has been set (at single ridge, the formation of the first spikelet), the time of flag leaf emergence, the time of jointing (internode elongation detected), and the number of spikelets on the spike can be computed. The number of spikelets is estimated before they form. If florets form at a constant rate, the possible number of them on each spikelet can also be computed. The earliest spikelet to reach double ridge is also the earliest to form florets; this spikelet is located about one-third of the way up from the base of the mature spike for wheat (Bonnett, 1966; Kirby, 1974). Each spikelet above the first to form florets is assumed to begin floret initiation as it reaches a comparable age. Those below form in a more or less symmetrical pattern with respect to those above the first spikelet to double ridge. The timing of formation of the first floret on these lower one-third spikelets is set by allowing the basal spikelet to form its florets at the same time as the terminal spikelet forms its florets. Those between the basal spikelet and the first to form florets begin their florets in a linear sequence interpolated between those two.

This tightly interwoven diagram implies the potential

number of spikelets on a wheat spike is determined by the combination of flag leaf number and the length of the phyllochron. Flag leaf number can range from 6 to 16 or more and phyllochron from 60 to 150 base 0°C degree-days. With each unit increase in the leaf number that represents the flag leaf, the spikelet number is expected to increase by two. With a leaf number of 15 for the flag leaf and a phyllochron of 130 degree-days, 26 spikelets are expected (Fig. 1a). With a leaf number of 7 for the flag leaf and a phyllochron of 70 degree-days, 11 spikelets are expected (Fig. 1b). Somewhat surprisingly, as the phyllochron interval increases, expected spikelet number decreases. For a plant where the flag leaf is Leaf Number 11 and the phyllochron is 80 degree-days, 20 spikelets are expected. With the same flag leaf number but a phyllochron of 120 degree-days, only 19 spikelets are expected.

In nature, the phyllochron and leaf number that is the flag leaf tend to change in concert, which tends to maintain a stable number of spikelets on the wheat spike. Phyllochrons of plants with a small number (6, 7, or 8) for the flag leaf are usually short (60–80 degree-days), and those of plants with a large number for flag leaf (12 or above) are usually long (100 degree-days or longer).

In Fig. 1, it has been assumed that one kernel is successful on the terminal spikelet, all kernels that are older than the terminal spikelet kernel survive, and all younger ones abort (Whingwiri and Stern, 1982). With this restrictive combination of simple assumptions, a lanceolate spike shape, similar to that of common wheat spikes, is predicted. The pattern of kernel formation was based on concepts and descriptions of Malvoisin (1984).

Similar diagrams can be provided for cereals with different spikelet-floret formation strategies than wheat. Barley, for example, is illustrated in Fig. 2 (Bonnett, 1966). Rice produces a branched panicle as illustrated (with alternate primary branches omitted from the drawing for clarity) in Fig. 3. The plastochron and phyllochron are the same interval for rice. Rice phytomer initiation and leaf extension are synchronized with a constant offset of five phyllochrons (or plastochrons) between them. In both wheat and barley, the *phytomer lifetime* (arbitrarily defined here as the interval between initiation of a phytomer and the completion of elongation of its leaf blade) is successively longer (in degree-days) for each successive phytomer. This contrasts with the constant phytomer lifetime for rice.

As was illustrated by Skinner and Nelson (1995), the development of each phytomer can be observed at the cellular level to reveal the sequence of cell division, elongation, and maturation that takes place among the cells of a phytomer and between phytomers. This information can be added to our diagram in the following manner. During the interval from one to two phyllochrons following initiation of each phytomer, the cells of the phytomer are dividing to form most of the cells that will make up the leaf blade and sheath. See the lightly shaded area in Fig. 4A. After the leaf blade of the phytomer has extended (the multiple phyllochron interval following blade extension, dark bricked area in Fig. 4A), no cells are dividing; most have expanded to their full length, and secondary internal processes are occurring. Between the lightly shaded and the dark bricked areas, the open brick shading represents the time interval when cells of the phytomers expand as described by Skinner and Nelson (1995) and as illustrated for rice by Matsuo and Hoshikawa (1993).

The position of these areas of cellular division, expansion, and maturation shown in Fig. 4A are approximations drawn by eye with straight lines. The test of relative reality of this representation can be illustrated in Fig. 4B. If a vertical section is drawn at a specific location on the time (degree-day) axis of the diagram, that section should trace a phytomer profile. This profile should present the stage of development at a cellular level for every phytomer of the plant. Such profiles could also be extended into the region of reproductive development.

The complete development diagram with cell condition

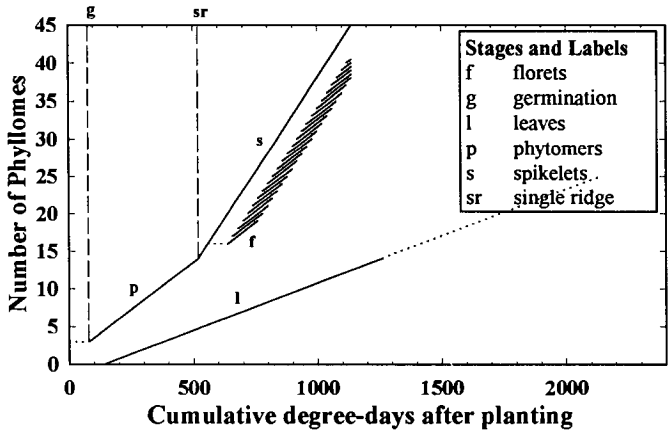

Fig. 2. Phyllome formation: phytomer and spikelet component appearance patterns for barley with a phyllochron of 80 degree-days and Leaf Number 14 as flag leaf.

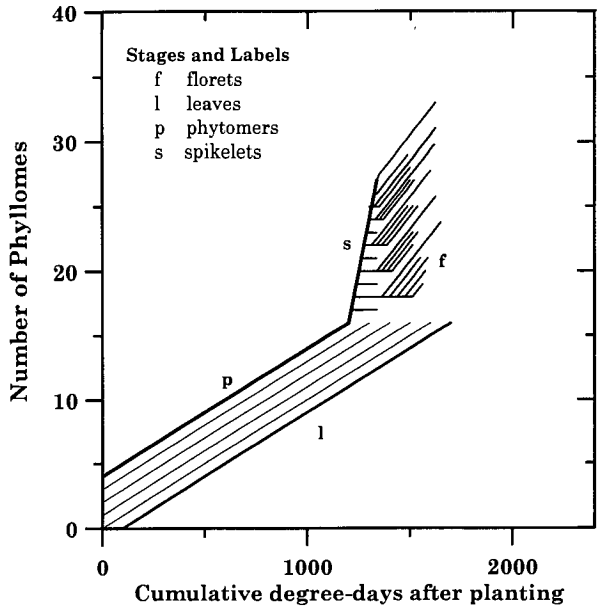

Fig. 3. Phyllome formation: phytomer and spikelet component appearance pattern for rice. Unspecified constant phyllochron assumed for illustration.

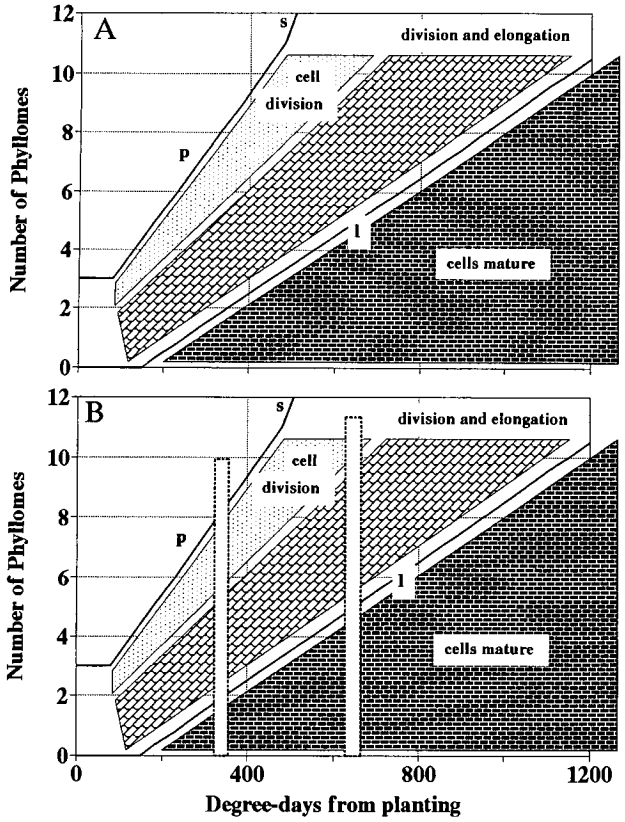

Fig. 4. (A) Phytomer cell maturation regions superimposed over the line segments representing phytomer formation (p), leaf appearance (l), and spikelet formation (s) of wheat. Phyllochron is unspecified. Leaf Number 11 is flag leaf. (B) Vertical sections representing arbitrarily chosen times show the expected cellular maturation of each phytomer at those times.

for the plant main stem is shown in Fig. 5. This diagram shows the synchrony of phytomer development within the developmental lifetime of each phytomer and among phytomers of the plant. Equally synchronous events, including root formation and branching and tiller formation and development, take place during phytomer development. For rice, all phytomers of the main stem, tiller bud initiation and extension, root bud formation and extension, and the complete sequence of events of the reproductive branches and subbranches have been described and illustrated at the cellular and appearance level (Matsuo and Hoshikawa, 1993). Rice provides the advantage for simplicity of description and of having the five relatively well-defined cellular development stages as illustrated in Fig. 3.

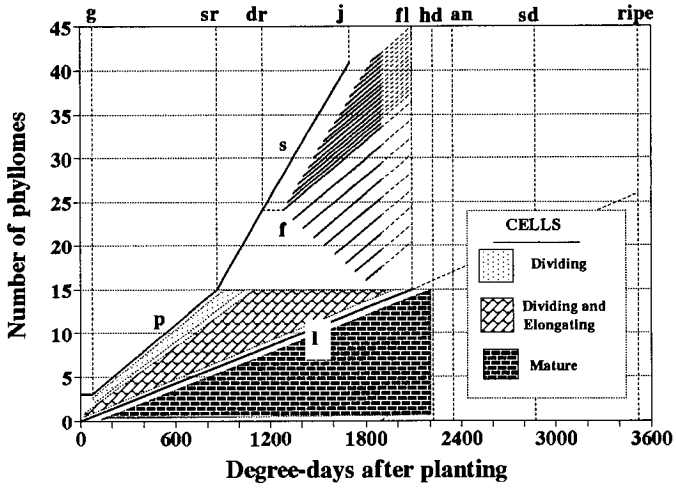

Fig. 5. Phyllome formation: phytomer and spikelet component appearance patterns for wheat with regions of different maturation for the cells of the phytomers included. Phyllochron is 130 degree-days and Leaf Number 15 is flag leaf.

Two further additions of descriptive information are possible with parts of the diagram of Fig. 5. Tiller formation is synchronized with the number of leaves that have extended on the main stem (Klepper et al., 1982) and can be represented as in Fig. 6. Both phytomer initiation and extension of the leaves for only the first three tillers are illustrated. If one were able to overlap the drawings without excessive confusion, the complete cell-detail representation of development that is included in Fig. 5 could be added for each tiller of Fig. 6. A vertical section through such a drawing should indicate the condition of development of the cells of each and every phytomer of every tiller represented.

The second piece of information that could be displayed by an extension of Fig. 6 relates to perennial forage grasses. As pointed out by Moore and Moser (1995), the perennial grasses maintain both living vegetative and reproductive culms at certain times of their development. Extending Fig. 6 to include the successive tillers in both reproductive and vegetative stage that form during a period of several years would be possible but would be cumbersome. Some approximation of such a diagram, restarted each spring, might help to understand which tillers form and mature sufficiently to become reproductive and which remain vegetative to carry the plant into the next year.

This discussion did not directly address the problem of finding the universally constant developmental timing interval or finding the unit that predicts its length in time, but hopefully, it does provide sufficient incentive to continue the search. If we are to progress, we must take advantage of our knowledge of genetically determined

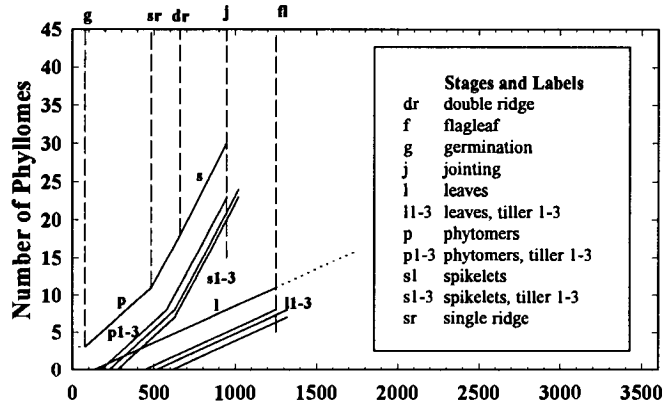

Fig. 6. Phyllome formation for main stem and tillers of wheat: Appearance of phytomer components and spikelets.

sensitivities. Both vernalization and day length sensitivity of cultivars used for developmental studies will influence the time of occurrence of reproductive developmental events. Multiple external factors cause deviations from the simple linear rates in the analysis presented above. Each of these (temperature change, day length change, solar radiation, water availability, nutrient level, seed bed temperature, development-stage-dependent base temperature, etc.) will have to be monitored in sufficient detail to determine short term rates as well as total amounts. Corrections for temperature extremes and their effects on the physiology of a plant as well as appropriate base and ceiling temperatures for thermal times as suggested by Bauer et al. (1984) will be needed. Developmental data sets will have to include both plastochron and phyllochron observations at frequent intervals if factors that influence their relative rates are to be determined. The rates of formation of spikelets and florets are also important to know because small changes in them can have a large impact on yield and manageable environmental factors can influence them; however, both are difficult, destructive, time consuming observations. The easy work seems to have been completed. Further progress will no doubt be slower, more difficult, and more expensive.

Cooperative effort must be utilized to obtain the needed information about environmentally dependent variation in the phyllochron and its related measures at a practical cost. With the known ranges of sensitivities to vernalization and day length of selected cultivars of genetic material available for experimentation, it would seem profitable to consider using similar cultivars across locations where adaptation permits. Also multiple cultivars with different sensitivities at any one site should be utilized. Perhaps such side by side and cooperative cross-site investigations can provide insights not otherwise gained.

During the search for a more nearly universal unit to measure a constant developmental timing interval, the developmental synchrony illustrated in Fig. 5 may still be used as a powerful quantitative tool for describing specific environmental and stress effects on cereal and noncereal grass shoot development. The diagram illustrates a simple but complete model of grass development. Genetic, environmental, and specific stress effects can be described by observed deviation from the model. Time of occurrence of developmental stages can be anticipated based on the model. Again, any deviations from the model should provide insight into the real operating mechanisms within the plant. Both research and production agriculture can benefit from projections of dates of development stages as a guide for timing observations or management practices.

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