

PHENOLOGY, DEVELOPMENT, AND GROWTH OF THE WHEAT (*Triticum aestivum* L.) SHOOT APEX: A REVIEW

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I. INTRODUCTION

So nature glories in her highest growth,
Showing her endless forms in orderly array.
None but must marvel as the blossom stirs
Above the slender framework of its leaves.

GOETHE

For centuries, people have studied the physiology and morphology of economic crops within the Poaceae family, with the result being perhaps the largest body of literature of any group of plants. Despite developmental and physiological differences, such as spike developmental patterns and C_3 and C_4 photosynthetic pathways, many similarities also exist among grasses, especially small-grain cereals

(Bonnert, 1966; Evans, 1940; Jeater, 1956, Rickman and Klepper, 1995). The objective of this paper is to review the vast literature on the development, phenology, and growth of the wheat shoot apex. Although focusing on wheat, other species are occasionally considered, and it is hoped that a greater understanding of grass shoot apex functioning is achieved.

II. GENERAL PATTERNS OF GRASS SHOOT APEX DEVELOPMENT

As any grass shoot apex begins development, leaf primordia are initiated with their associated axillary bud (Fig. 1). The leaf, axillary bud, and node plus internode are referred to as a phytomer unit (Wilhelm and McMaster, 1995). The grass shoot is composed of the repeated addition of phytomer units, and therefore the phytomer unit is the basic building block of grass canopies (Rickman and Klepper, 1995; Wilhelm and McMaster, 1995). A wide variety of biotic (e.g., genetics, weeds, and disease) and abiotic factors (e.g., temperature, water, nutrients, light, and CO₂) influence the further differentiation and growth of the phytomer unit.

Shoot apices at some later time may initiate floral structures. Each grass species differs slightly on how the floral structures develop, but normally these structures develop from the axillary bud. Evans (1940) gives a concise summary of the work of Trecul and Goebel that delineates the three patterns of developmental succession of lateral primordia on the incipient inflorescence of grasses. Wheat fits under the pattern in which inflorescence primordia are initiated acropetally and subsequent development is fastest in the central region of the inflorescence and differentiation occurs basipetally and acropetally from this point.

Each shoot apex exhibits varied degrees of coordination of development and growth with other shoot apices within a plant. Plant form can then be viewed as the net birth and death of phytomer units, modified by growth rate and form of the phytomer unit, and population ecology concepts can then be applied. The summation of all shoot apices, and the phytomer subunits, on different plants results in the population patterns unique to the species and its environment. Because ecological plant morphology lies outside the domain of this review, no more will be said here; however, further information may be found in Dirzo and Sarukhan (1984).

III. MORPHOLOGICAL NOMENCLATURES

The development of morphological nomenclatures in the past half century has facilitated the study of plant development. A variety of methods have been pro-

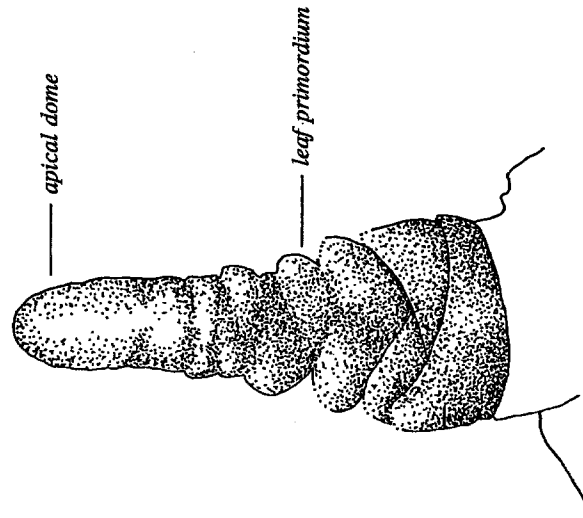


Figure 1. Drawing of a wheat shoot apex at single-ridge growth stage. Leaf primordia are initiated acropetally on the shoot apex; axillary buds (not discernible in this drawing) would form on the abaxial base of the leaf primordium. Being at the single-ridge growth stage, the apical dome has elongated and the younger leaf primordia will not grow further.

posed, and subsequently modified, for naming various aboveground plant organs and defining stages of phenological development (e.g., Bruns and Croy, 1983; George, 1982; Haun, 1973; Lancashire *et al.*, 1991; Large, 1954; Noda *et al.*, 1993; Robertson, 1968; Tottman and Makepeace, 1979; Waldren and Flowerday, 1979; Zadoks *et al.*, 1974). Morphological naming schemes for wheat plant structures have not had universal acceptance and have just recently become more widely used.

Jewiss (1972) and Klepper *et al.* (1982, 1983a) proposed a simple leaf-naming convention in which true leaves are numbered acropetally for each culm. The first foliar leaf on a culm is designated L1, followed by L2, L3, etc. Haun (1973) devised a growth staging system that allows the total number of leaves on a culm to be incorporated into the vegetative stages:

$$\text{Haun stage} = (n - 1) + \frac{L_n}{L_{n-1}}, \quad \left(0 < \frac{L_n}{L_{n-1}} \leq 1 \right)$$

where n is the number of leaves that have appeared on the culm, L_{n-1} is the blade length of the penultimate leaf, and L_n is the blade length of the youngest visible leaf extending from the enclosing sheath of the penultimate leaf.

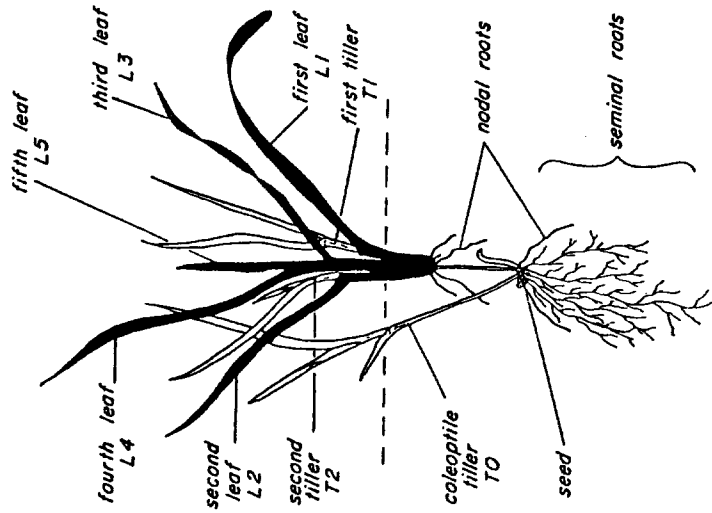


Figure 2. Drawing of a young wheat plant showing identified leaves, tillers, and roots. From Klepper *et al.* (1982). Reproduced with permission of Elsevier Science. Nomenclature is defined in the text.

Jewiss (1972) also developed a system for naming tillers on annual grasses, which has been modified and extended (Fraser *et al.*, 1982; Kirby *et al.*, 1985a; Masle, 1985; Masle-Maynard and Sebillotte, 1981a). One increasingly used system (Klepper *et al.*, 1982, 1983a) identifies tillers according to the leaf axil and parent culm with which the tiller is associated (Fig. 2). The first culm that emerges from the seed is the main stem (MS). All remaining culms are primary, secondary, tertiary, etc. tillers. Primary tillers are those culms that appear in the axils of MS leaves and are given one-digit designations following a "T," signifying "tiller." An example would be T1, which appears in the axil of L1 on the MS. Secondary tillers, or culms that appear in the axils of primary tiller leaves, are given two-digit designations. The first digit refers to the number of the parent primary tiller; the second digit refers to the parent primary tiller leaf subtending the secondary tiller. For example, T21 is a secondary tiller that appears in the axil of the first leaf (L1) of the primary tiller T2. In a similar manner, tertiary tillers are given three-digit designations (e.g., T211). The coleoptile tiller, born in the axil of the coleoptile leaf,

is designated T0 (Klepper *et al.*, 1982, 1983a; McMaster *et al.*, 1994) or TC by others (Kirby and Appleyard, 1987; Kirby and Eisenberg, 1966).

Most morphological naming schemes have been restricted to vegetative organs. Klepper *et al.* (1983b) proposed a numerical index for developmental stages of the spike, further extending other phenological growth-stage scales. Wilhelm and McMaster (1996) suggested a naming scheme for the spikelet, floret, and kernel components of a spike inflorescence. For each culm, the first spikelet at the base of the rachis is designated S1. Spikelets are sequentially incremented acropetally on the rachis (e.g., S2, S3, S4, etc.). Each floret or caryopsis position within a spikelet is sequentially numbered from base to apex as well. For example, the first floret position at the basal end of the rachilla is F1 (or C1 if the caryopsis), followed by F2/C2, F3/C3, etc. To uniquely identify a specific floret or caryopsis, the spikelet position and floret/kernel position are combined. For example, S3F2 would be the third spikelet from the base of the rachis and the second floret position from the base of the rachilla. The culm designation can be added at the beginning to uniquely identify each floret on any plant.

IV. SHOOT APEX DEVELOPMENTAL SEQUENCE

The preceding morphological naming schemes allow nondestructive identification of specific shoots but give no information regarding the developmental sequence and timing of events occurring within each shoot apex. Many important developmental events are not observable without magnification after plant dissection. Figure 3 (McMaster *et al.*, 1992b) illustrates the complete developmental sequence and timing for a generic winter wheat shoot apex. Duration of various stages can vary significantly among cultivars and with stresses (e.g., Fisher, 1973; McMaster *et al.*, 1992a,b; Saini and Tandon, 1983; Wang, 1960; Wilhelm *et al.*, 1993).

A. SHOOT APEX PHENOLOGY

Bauer *et al.* (1983) and Landes and Porter (1989) discuss commonly used phenological growth-stage scales and their relationships to each other for wheat. However, it is often difficult to compare data using different scales. Harrell *et al.* (1993) developed a computer program that converts between three phenological growth scales: Feekes (Large, 1954), Zadoks-Chang-Konzak (1974), and Haun (1973). These scales concentrate exclusively on growth stages visible without dissection. Therefore, stages such as single ridge, double ridge, start of internode elongation, terminal spikelet initiation (TS), and beginning of floret primordium initiation are

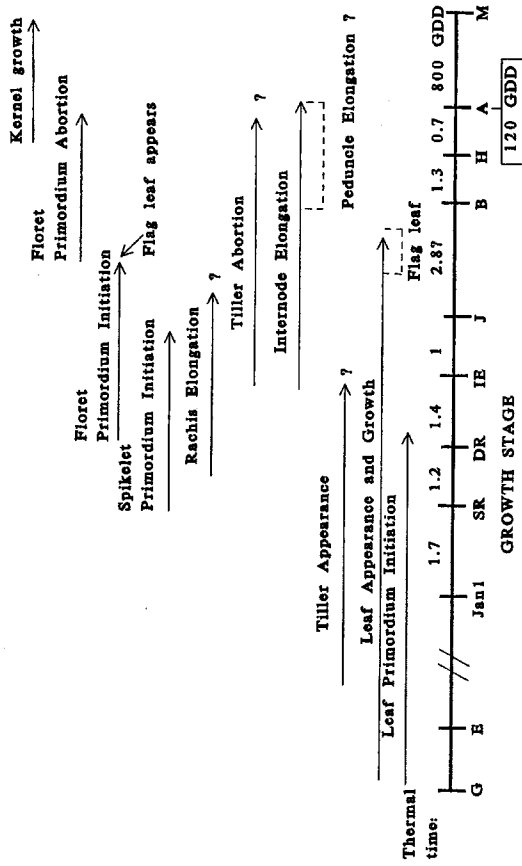


Figure 3. Culm developmental sequence and timing. Developmental sequence of the shoot apex related with phenological growth stages: germination (G), seedling emergence (E), double ridge (DR), jointing (J), heading (H), anthesis (A), and physiological maturity (M). Leaf appearance is the time when the youngest expanding lamina can be seen emerging from the enclosing penultimate leaf. Question marks indicate areas of uncertainty or variability due to cultivars, whether winter or spring wheat, environment, or conflicting reports in the literature. Thermal time is either in phyllochrons or growing degree-days and assumes optimal conditions. Adapted from McMaster *et al.* (1992b).

not considered. No scale has all the stages that are part of shoot apex development shown in Fig. 3.

The Feekes scale is commonly used to describe many of the externally visible growth stages for the main stem, with some of the stages more clearly defined. Jointing (stage 6) begins when the first node is 25 mm above the soil surface (Fig. 4). Booting (stage 10) begins when the flag leaf sheath completes growth and the spike is swollen but not yet visible within the flag leaf sheath. Because the beginning of booting is difficult to discern with confidence, I suggest a more useful definition is when the flag leaf collar is formed. Heading (stage 10.1) commences when the spike is first visible through the split in the flag leaf sheath or emerges from the collar of the flag leaf. For applicability to all varieties, I suggest that you must be able to see the glumes, paleas, or lemmas, and not just the awns, if using a cultivar with awns. Anthesis (stage 10.5.1) starts when the first anthers emerge from the spike and ends when anthers stop emerging. Physiological maturity (stage 11.4) is when grain dry weight reaches its maximum, which is correlated to the absence of green color in the chaff or kernels (Hanft and Wych, 1982; Singh *et al.*, 1984).

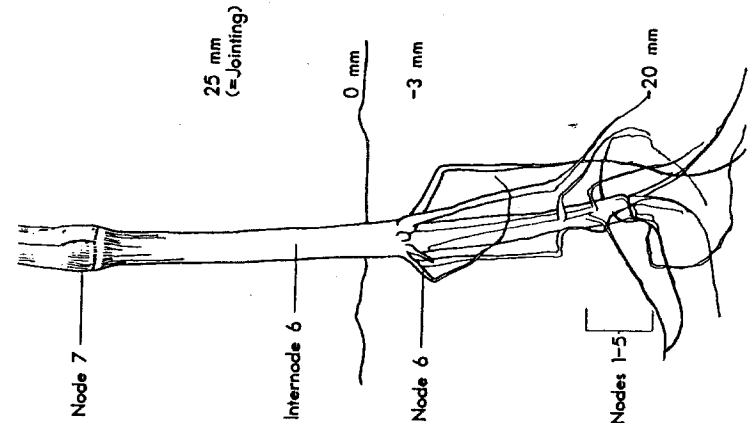


Figure 4. Diagram of identified nodes and associated internodes and definition of jointing growth stage. In this example, the elongation of internodes 5 and 6 raises the 7th node 25 mm above the soil surface, resulting in jointing as defined by the Feekes scale (Large, 1954). From McMaster *et al.* (1991). Reproduced with permission of Cambridge University Press.

Other phenological stages observable only after dissection, and usually requiring magnification, are defined as follows. Single ridge begins when the shoot apex first elongates (Fig. 1). Leaf primordia formed after this point do not differentiate further and grow into a single ridge around the elongated apex, which gives rise to its name (Fisher, 1973; Williams, 1966b). Double ridge commences when both leaf and spikelet initials appear as double ridges around the shoot apex (Fig. 5). The lower ridge is the leaf primordium, which does not develop further, and the upper ridge is the spikelet primordium (Barnard, 1955; Bonnett, 1966; Fisher, 1973; Oosterhuis and Cartwright, 1983; Williams, 1966b). The leaf initials subtending the spikelet primordia become progressively less developed toward the apex until the youngest leaf initials may consist of only a single cell division (Barnard, 1955; Williams, 1966b). Terminal spikelet stage is reached when the terminal spikelet initial is formed. Internode elongation begins when the first inter-

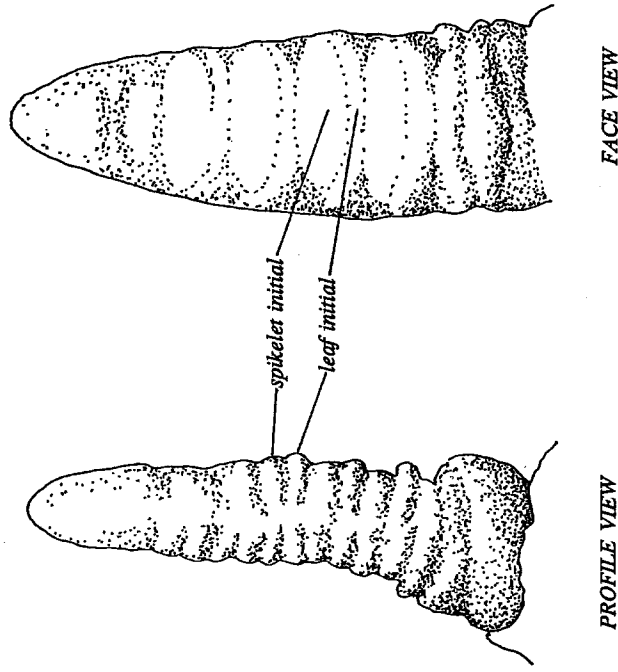


Figure 5. Drawing of a wheat shoot apex at double-ridge growth stage. Leaf and spikelet primordia are initiated acropetally on the shoot apex. The spikelet primordia will continue to differentiate and grow, but the leaf primordia will not. Profile view is viewing the apex at 90° rotation from the plane of leaves; face view is rotated 90° from profile view.

calary meristem initiates elongation in the spring and is associated with the onset of spike differentiation (Williams, 1966b).

An obvious conclusion from Fig. 3, but one that merits mentioning, is that externally visible stages are not often very well correlated with shoot apex development and the internal initiation of spikelet and flower primordia.

Phasic development is controlled by genetics and regulated by the environment. The usual approach for predicting phenological growth stages is empirically based using number of calendar days (ND), growing degree-days (GDD), or photothermal units (PTU) after considering the genetic tendencies of the crop or cultivar (e.g., Amir and Sinclair, 1991; Bauer *et al.*, 1986; Davidson and Campbell, 1983; del Pozo *et al.*, 1987; Hay and Kirby, 1991; Masoni *et al.*, 1990; Mor and Aggarwal, 1980; Nuttonson, 1955; Robertson, 1968; Slafer and Rawson, 1995; Travis and Day, 1988). Many criticisms have been directed toward these three models (e.g., McMaster and Smika, 1988; Shaykewich, 1995; Wang, 1960), but for wheat few other approaches have been developed and those that have may not have greater accuracy. The popularity of GDD and PTU models undoubtedly is due to

both the simplicity of the models and the overriding significance of temperature (and light for certain stages and cultivars) on wheat phenology (e.g., Allison and Daynard, 1976; Amir and Sinclair, 1991; Bauer *et al.*, 1986; Davidson and Christman, 1984; Davidson *et al.*, 1985; Halse and Weir, 1970; Hammes and Marshall, 1980; Kirby and Appleyard, 1984; Loss *et al.*, 1990; Marcellos and Single, 1971, 1972; Masle *et al.*, 1989a,b; Masle-Maynard, 1981a; McKinney and Sando, 1935; Ommrod, 1963; Pinthus and Nerson, 1984; Slafer and Rawson, 1994, 1995; Wall and Cartwright, 1974). Bauer *et al.* (1988) have suggested that the evidence that photoperiod affects winter wheat development rate independent of air temperature for the Great Plains is inconclusive.

Although temperature and light primarily control wheat phenology and development, water and nutrients do play a lesser role. Most studies show that water availability clearly influences phenology and development (e.g., Angus and Moncur, 1977; Baker *et al.*, 1986; Bauer *et al.*, 1985; Davidson and Chevalier, 1992; Frank *et al.*, 1987; McMaster and Smika, 1988; Nuttonson, 1955; Singh *et al.*, 1984; Sionit *et al.*, 1980); however, not all phenological stages seem to be significantly affected by water availability (Bauer *et al.*, 1984; Bingham, 1967; Davidson and Campbell, 1983; Doraiswamy and Thompson, 1982; Frank *et al.*, 1987). Salinity, which can impose a water stress effect on the plant, has also been shown to hasten phenology of at least certain growth stages, especially reproductive stages (Grieve *et al.*, 1993; Maas and Grieve, 1990; Maas and Poss, 1989). Generally, the pattern is that water stress hastens phenological timing (McMaster and Smika, 1988; McMaster *et al.*, 1992b).

The significance of nutrient availability on phenology and development is less clear. Studies can be found suggesting nutrient availability affects phenology and development (e.g., Bauer *et al.*, 1985; Birch and Hong, 1990; Blacklow and Incoll, 1981; Erdei *et al.*, 1986; Frank and Bauer, 1982; Frank *et al.*, 1987; Halse *et al.*, 1969; Holmes, 1973; Longnecker *et al.*, 1993; Nerson *et al.*, 1990; Nuttonson, 1955; Whingwiri and Stern, 1982), whereas others find no significant effect on phenology and development (e.g., Bauer *et al.*, 1984; Belford *et al.*, 1987; Bingham, 1967; Davidson and Campbell, 1983; Frank and Bauer, 1982; Langer and Liew, 1973; Longnecker *et al.*, 1993; McMaster and Smika, 1988; Nuttonson, 1955; Single, 1964; Whingwiri and Stern, 1982). A number of factors contribute to the uncertainty of the role of nutrients. First, there is great variation in cultivar response to nutrients. Second, different stages seem to be affected more than others, and this varies with the nutrient. Nitrogen has less effect on vegetative phases than on spikelet, floret, and grain development phases (Bauer *et al.*, 1985; Frank and Bauer, 1982; Longnecker *et al.*, 1993; Whingwiri and Stern, 1982). Third, most studies start with different nutrient levels, but as time progresses it becomes unclear what level of nutrient stress exists. Nutrient cycling in the soil and storage in plant tissue both contribute to uncertainty on nutrient availability later in the life cycle. Lastly, different nutrient levels are tested, and some levels probably exceed

a threshold of nutrient stress resulting in no significant plant response. As Bauer *et al.* (1985) discuss for N, the interaction of soil N levels and soil water results in little consistency of plant developmental and phenological response to a given N fertilizer rate. Both water and nutrient effects on phenology and development are also confounded by their potential indirect effects on the microenvironment, particularly on meristem temperature and within canopy light quality and intensity. Previous studies have not evaluated how water and nutrients may alter the microenvironment. McMaster and Smika (1988) suggested little is to be gained in accuracy of empirical phenological models by considering N status.

Other factors may also play a secondary role affecting phenological development. For instance, doubling ambient CO₂ has been reported to slightly shorten the time to reach various growth stages such as floral initiation and anthesis (LeCain *et al.*, 1992; Marc and Gifford, 1984), regardless of culm considered, although Gifford (1977) found no effect of enhanced CO₂, and under certain conditions of depleted CO₂ levels found that anthesis was reached earlier.

The ND, GDD, and PTU models often do not predict growth stages near jointing well for winter wheat (McMaster and Smika, 1988; McMaster *et al.*, 1992b) because they do not account for vernalization. The gene symbol Vrn is given to the system of genes responsible for sensitivity to vernalization (Stelmakh, 1987). The presence of dominant alleles at one or more loci results in partial or complete inhibition of the vernalization requirement. Vernalization is a complex process with many factors interacting (Purvis, 1961). Although many have tried to quantify vernalization responses, generally quantitative methods to predict vernalization are lacking (Ahrens and Loomis, 1963; Craigon *et al.*, 1995; Trione and Metzger, 1970).

Cultivars vary greatly in their vernalization requirements (e.g., Craigon *et al.*, 1995; Davidson and Christian, 1984; Davidson *et al.*, 1985; Evans and Wardlaw, 1976; Flood and Halloran, 1986; Gardner and Barnett, 1990; Gott, 1961; Halse and Weir, 1970; Mosaad *et al.*, 1995; Slafer and Rawson, 1994; Stelmakh, 1987; Wall and Cartwright, 1974; Yasuda, 1984). A number of environmental factors, particularly photoperiod and temperature pattern, interact variably with cultivars to confound the vernalization response (Davidson *et al.*, 1985; Purvis, 1961; Salini and Tandon, 1989). Even many spring wheats that do not require vernalization to enter the reproductive phase still respond positively to cold temperatures (Evans and Wardlaw, 1976; Halloran, 1977; Jedel *et al.*, 1986; Levy and Peterson, 1972). Vernalization response also seems to influence the duration of phenological growth stages and rates of primordium initiation (Cutforth *et al.*, 1992; Flood and Halloran, 1986).

One rarely attempted approach for estimating the time between various growth stages is to use the phyllochron concept (Fig. 3; McMaster *et al.*, 1992b; Rickman *et al.*, 1996). The phyllochron is the thermal time it takes for successive leaves on a shoot to reach the same developmental stage. If thermal time is measured in ac-

cumulated growing degree-days, then the phyllochron is very similar to the GDD model. However, factors that change the phyllochron are automatically incorporated into the rest of the phenological development scheme. For example, inverse relationships between planting date and time to growth stage have been reported (e.g., Fischer and Kohn, 1966; Ghadekar *et al.*, 1992; Hay, 1986; Kirby and Appleyard, 1987; Nuttonson, 1948; Pinthus and Sar-Shalom, 1978). Given that the phyllochron usually decreases with later planting dates (Baker *et al.*, 1980; Stern and Kirby, 1979), the phyllochron approach should more accurately respond to this trend rather than the static GDD approach.

Few estimates of the number of phyllochrons between phenological growth stages are reported in the literature. Rickman and Klepper (1991), Kirby *et al.* (1993), and McMaster *et al.* (1992b) give some estimates for winter wheat cultivars with moderate photoperiod sensitivity that are fully vernalized, and Frank and Bauer (1984) and Gardner *et al.* (1985) discuss a few intervals for spring wheat cultivars.

The preceding discussion of phenology has generally pertained to the main stem. However, not all culms on a plant reach the same growth stage simultaneously. Normally, successively younger and smaller culms reach the same phenological growth stage later. The stagger among culms tends to be reduced as the plant approaches maturity (Baker and Gallagher, 1983a; Stern and Kirby, 1979; Whingwiri and Stern, 1982). Hay and Kirby (1991) review how the convergence of development of successively initiated organs, or of different sowing dates, results in particular stages occurring in the plant or throughout the crop in synchrony within a few days.

B. SHOOT APEX DEVELOPMENTAL EVENTS

The developmental events depicted in Fig. 3 are discussed below in approximate sequential order. The justification for the sequence and reasons for the question marks are presented in the appropriate sections.

1. Leaf Primordium Initiation

Evans (1940) and Wilhelm and McMaster (1995) outline the history of the plastochron dating back to 1873. Originally, the plastochron had a much more general meaning of the interval of time between two recurring successive events, such as leaf or flower initiation (Hill and Lord, 1990). Today, the plastochron is commonly used as the thermal time between the appearance of successive leaf primordia on a shoot (Fig. 1; Erickson and Michelini, 1957; Lamoreaux *et al.*, 1978; Wilhelm and McMaster, 1995) and is distinguished from the phyllochron, which is the thermal time between the appearance of successive leaves on a shoot (Klepper

per *et al.*, 1982; Wilhelm and McMaster, 1995). Generally, primordia are initiated at about twice the rate of the phyllochron (e.g., Baker and Gallagher, 1983b; Delecolle *et al.*, 1989; Kirby, 1985, 1995; Kirby and Appleyard, 1987; Malvoisin, 1984), and at a linear rate with growing degree-days (Gallagher, 1979; Grieve *et al.*, 1993; Hay and Wilson, 1982; Malvoisin, 1984). About 0.03 leaf primordia per day are initiated for each degree rise in temperature above the base temperature (0°C), or about 0.4 leaf primordia per day at 15°C (Baker and Gallagher, 1983b). Temperatures above about 30°C retard leaf primordium initiation (Friend *et al.*, 1963). Vernalization and photoperiod have little effect on the plastochron; however, because vernalization and photoperiod affect the duration of initiation of leaf primordia, these factors will affect the final number of leaf primordia (Kirby, 1985). Friend *et al.* (1963) reported that light intensity increased the plastochron, but they did not measure shoot apex temperature.

About three or four leaf primordia are present in the seed embryo (Baker and Gallagher, 1983a; Bonnett, 1966; Bradbury *et al.*, 1956; Hay and Kirby, 1991; Kirby and Appleyard, 1987; Lersten, 1987; Malvoisin, 1984; Williams, 1975), and nearly half the final number of leaf primordia have been initiated by seedling emergence (Baker and Gallagher, 1983b; Hay and Kirby, 1991). Leaf primordia form in the two-layer tunica region of the shoot apex (Barnard, 1955).

2. Tiller or Axillary Bud Initiation

The axillary bud, also called the tiller bud, appears somewhat later than the associated leaf primordium (Longnecker *et al.*, 1993). Baker and Gallagher (1983a) could find no tiller bud primordium associated with leaves higher than L7 or L8, although the main stem had 12 leaves. It is likely that the axillary buds associated with leaves L9–L12 were insufficiently differentiated to be detectable.

3. Leaf Primordium Elongation

Wheat leaf ontogeny follows a similar pattern regardless of leaf position, even though leaf development is heteroblastic between the first two true foliar leaves of the main stem (Engledow and Ramiah, 1930; Klepper *et al.*, 1983a). In wheat leaves, the upper leaf zone (oberblatt) has been eliminated. The blade and sheath components are combined into the lower leaf zone, or unterblatt. The wheat phytomer unit follows the pattern of development typical of grasses in which the leaf blade begins growing first, followed by sheath growth, then internode elongation (Ettler, 1951; Nemoto *et al.*, 1995; Skinner and Nelson, 1995). Early in primordial development, an intercalary meristem is created that separates into two regions: The proximal region gives rise to the sheath and the distal region creating the lamina (Dale, 1988). Cells enlarge rapidly once they are not in the meristematic region (Dale, 1988). Four distinct development stages of tall fescue leaf blades (*Fes-*

tuca arundinacea Schreb.) have been described: formation of the epidermal cell division zone, formation of the epidermal cell elongation zone, linear elongation phase, and cessation of elongation due to no new cell division and existing cells being fully elongated (Skinner and Nelson, 1995). Decreasing irradiance reduces the growth zone of elongating leaves (Sanderson and Nelson, 1995). Blade growth rates change during the ontogeny of the leaf, with maximum elongation rates a few days before the blade emerges from the penultimate leaf sheath (see Skinner and Nelson, 1995, for tall fescue; Williams, 1975; Williams and Rijken, 1965). Rates for corresponding phases tend to decrease and the duration of the phases increases as later leaves commence elongation.

Leaf appearance rates are slower than primordium initiation rates (e.g., Baker and Gallagher, 1983b; Delecolle *et al.*, 1989; Kirby, 1985, 1995; Kirby and Appleyard, 1987; Malvoisin, 1984), and not all leaf primordia develop fully into leaves. Flag leaf number is determined at single ridge because all leaf primordia that are present as single ridges around the apex do not further differentiate and grow; flag leaf number is about twice the main stem Haun at single ridge (Rickman and Klepper, 1991), although this is assuming "normal" planting dates and environmental conditions.

The phyllochron has been examined for various cultivars of small-grain cereals since 1960. The phyllochron seems similar for all culms within a plant, although some studies have found tillers, especially the coleoptilar tiller, to have different phyllochrons than the main stem (Anslow, 1966; Cannell, 1969; Fletcher and Dale, 1977; Kirby and Appleyard, 1987; Kirby and Riggs, 1978; Kirby *et al.*, 1985b; Longnecker *et al.*, 1993; Peterson *et al.*, 1982; Rawson, 1971a). Normally, the phyllochron appears relatively constant during the growing season when plotted as a function of growing degree-days (e.g., Baker *et al.*, 1980; Belford *et al.*, 1987; Cao and Moss, 1991; Delecolle *et al.*, 1989; Friend, 1965b; Hunt and Chapleau, 1986; Kirby, 1993, 1995; Kirby and Appleyard, 1987; Kirby and Eisenberg, 1966; Kirby *et al.*, 1982, 1989; Kirby and Perry, 1987; Klepper *et al.*, 1982, 1983a; Krenzer *et al.*, 1991; Longnecker *et al.*, 1993; Malvoisin, 1984; Masle *et al.*, 1989b; Masle-Maynard, 1981b; Mosaad *et al.*, 1995; Rawson *et al.*, 1983; Wiegand *et al.*, 1981). However, very detailed examination of the phyllochron, particularly in growth chamber studies, shows that the phyllochron is curvilinear with temperature (Baker *et al.*, 1986; Cao and Moss, 1989a; Hay and Delecolle, 1989). Indeed, when examining many of the experiments that report linearity, a slight sigmoidal pattern can often be detected, particularly a slight increase in the phyllochron after about the 3–5 leaf stages. Two factors could explain this: a decrease in temperature as winter approaches, thus causing an increase in the phyllochron, and the three or four leaf primordia present in the seed embryo will have elongated and the remaining leaves must come from primordia initiated after germination. With rice, Nemoto *et al.* (1995) report that the phyllochron is greater for the last four or five leaves to appear. This change has been associated with inflorescence initiation and

internodal elongation, both of which are occurring simultaneously. Another possible factor impacting the phyllochron is the length of the whorl that the elongating leaf must pass through, which increases until internode elongation begins, resulting in a shorter distance (Miglietta, 1991a; Skinner and Nelson, 1995). However, if this is a major factor, then Nemoto *et al.* (1995) should not have found a greater phyllochron for the last four or five leaves to appear in rice when internode elongation was occurring. Although this issue is interesting theoretically and important in understanding factors controlling the phyllochron, under most field conditions the phyllochron can reasonably be assumed to be linear with growing degree-days.

Occasionally, the phyllochron shifts in the spring for unknown reasons (Baker *et al.*, 1986; Grieve *et al.*, 1994; Cao and Moss, 1991; Hay and Delecolle, 1989). For field conditions, the shift (both increase and decrease) occurs shortly before or near double ridge but varies depending on planting date, and the shift is correlated with a change in the primordium initiation rate (Hay and Delecolle, 1989).

The phyllochron varies among cultivars (e.g., Anslow, 1966; Baker *et al.*, 1986; Frank and Bauer, 1984; Kirby *et al.*, 1985a; Kirby and Perry, 1987; Mosaad *et al.*, 1995; Syme, 1974). There appears to be little or no relationship between the phyllochron and maturity class, semidwarfing genes, or degree of vernalization requirement (McMaster *et al.*, 1992b; Mosaad *et al.*, 1995). Information is currently insufficient to model or predict cultivar-related differences.

Temperature and photoperiod are the major factors controlling leaf and tiller appearance, but other factors, such as nutrients, water, salinity, CO₂, light intensity and quality, vernalization, seed size, planting depth, and soil strength, may effect the phyllochron (e.g., Anslow, 1966; Cutforth *et al.*, 1992; Kirby, 1993; Masle and Passioura, 1987; Rickman and Klepper, 1995; Wilhelm and McMaster, 1995). Under controlled conditions, Longnecker *et al.* (1993) showed a positive correlation between the phyllochron and available N, with a more pronounced effect on tillers, although there was a cultivar response. Dale and Wilson (1978) reported similar results to those of Longnecker *et al.* (1993) for barley in sand culture. Belford *et al.* (1987) found that only younger, higher-order tillers showed slight effects of N on leaf development rates. Single (1964) showed a decrease in final leaf number as N levels decreased; presumably, the duration of leaf appearance, rather than the rate of leaf appearance, was shortened by low N levels. Other studies have found no effect on N on the phyllochron (Maan *et al.*, 1989; G. S. McMaster, unpublished data, also for P and Zn). It appears that unless N is very limiting, there is little effect on the phyllochron. The role of other nutrients has been studied rarely, if at all.

Baker *et al.* (1986) observed a shorter phyllochron under dryland conditions than under irrigated conditions. Unpublished data from South Africa (S. Walker, 1990–1992) showed a 10% decrease in the phyllochron under dryland conditions when compared to irrigated conditions. Cutforth *et al.* (1992) showed that severe

water stress increased the phyllochron. Krenzer *et al.* (1991) found a slight increase in the phyllochron with water stress. Salinity has been reported to increase the phyllochron (Grieve *et al.*, 1994; Maas and Grieve, 1990). Unfortunately, almost all water stress studies have not measured canopy or shoot temperature.

LeCain *et al.* (1992) have shown a decrease in the phyllochron under conditions of increased canopy CO₂ concentrations, whereas Gifford (1977) reported no effect. Rickman *et al.* (1985b) showed an increase in the phyllochron with an increase in photosynthetic photon flux densities under light-limiting conditions, as did others (Barnes and Bugbee, 1991; Bugbee and Salisbury, 1988; Friend *et al.*, 1963; Masle *et al.*, 1989b). Friend *et al.* (1962) did not find a photoperiod effect on the phyllochron, but others (Cao and Moss, 1989b; Kirby and Eisenberg, 1966) have found a photoperiod effect. Light quality (R/FR ratio) has been shown to have a slight negative correlation with the phyllochron (Barnes and Bugbee, 1991; Bugbee and Salisbury, 1988; Skinner and Simmons, 1993). Seed size is positively correlated with the phyllochron (Peterson *et al.*, 1989), and planting depth (Kirby, 1993) and soil strength (Masle and Passioura, 1987) are negatively correlated.

These conflicting results on factors influencing the rate of leaf appearance can perhaps be reconciled by first discerning primary and secondary factors and then determining when the factors are influential. It seems clear that temperature is the primary factor driving the rate of leaf appearance, with light (quantity, quality, and photoperiod) also very important (Anslow, 1966; Cao and Moss, 1989a,b,c; Dale, 1988; Frank and Bauer, 1995; Friend *et al.*, 1963; Kirby and Eisenberg, 1966; Langer, 1979; Masle *et al.*, 1989a; Porter and Delecolle, 1988). Other factors discussed previously are secondary factors that only become influential when very limiting or for certain cultivars. It is unknown if these factors are delaying the development of the leaf primordium or, more likely, if they are decreasing the rate of blade elongation, which would delay the appearance of the leaf from the subtending sheath.

Baker *et al.* (1980) were the first to report an equation to predict the phyllochron for wheat. They reported a linear relationship between the change in photoperiod following seedling emergence and the phyllochron. Others (Belford *et al.*, 1987; Delecolle *et al.*, 1985, 1989; Kirby, 1995; Kirby and Eisenberg, 1966; Kirby and Perry, 1987; Kirby *et al.*, 1982, 1985a; Malvoisin, 1984; Masle *et al.*, 1989b; McKinney and Sando, 1935; Rickman and Klepper, 1995) have reported results supporting Baker *et al.* (1980). The correlation is indirectly supported by many studies showing a relationship between leaf development rates and sowing date or photoperiod (Baker *et al.*, 1980; Hay and Wilson, 1982; Kirby and Perry, 1987; Kirby *et al.*, 1982, 1985a; Mosaad *et al.*, 1995). Results such as these have led many scientists to view the phyllochron as being relatively "fixed" by the environment in which the seedling germinates. Inconsistencies with this viewpoint arise from many directions. The relationship between change in day length at seedling emergence and the phyllochron involves much variation, and as Delecolle

et al. (1985) point out, measurement errors could account for much of the variation. This correlation also does not seem to exist in greenhouse and growth chamber experiments (Cao and Moss, 1989a,b,c, 1994; Friend *et al.*, 1962; Hay and Delecolle, 1989; Judel and Mengel, 1982; Kirby *et al.*, 1983). Unexplainable shifts of the phyllochron can occur, and indeed the phyllochron often is not constant during the growing season or is different at constant temperatures or photoperiods. Clearly, the correlation between change in day length at seedling emergence and the phyllochron is merely an environmental cue that we can determine but is not the actual cause "setting" the phyllochron shortly after emergence, if indeed it is set at all. Cao and Moss (1994) hypothesized why the constant phyllochron for a planting date relationship is found. They note that the phyllochron responds nonlinearly to temperature and photoperiod but is constant within a constant temperature or photoperiod. Under field conditions in which temperatures and photoperiods vary, but generally are increasing or decreasing depending on time of year, there is differential response of the phyllochron based on the conditions. Temperature and photoperiod during the growing season can offset each other, resulting in a constant phyllochron for a planting date. Shifts in the phyllochron could be caused by unseasonably high or low temperatures disrupting the normal temperature:photoperiod relationship. Jamieson *et al.* (1995) also attempted to explain the observed relationship between the phyllochron and emergence date by basing the phyllochron on apical temperature (or near-surface soil temperature) rather than on air temperature.

Efforts to use the relationship presented by Baker *et al.* (1980) between phyllochron and change in day length at the time of seedling emergence have met with some success. The relationship has been used in wheat simulation modeling efforts for English and U.S. growing conditions and had satisfactory results (McMaster *et al.*, 1991, 1992a,b; Rickman *et al.*, 1996; Weir *et al.*, 1984; Wilhelm *et al.*, 1993).

Subsequent to Baker *et al.* (1980), other equations have been published to predict the phyllochron. Kirby and Perry (1987) used the same concept as Baker *et al.*, but based their coefficients on Australian cultivars and conditions. Cao and Moss (1989a,b,c) used a curvilinear relationship for the effects of temperature, photoperiod, and temperature by photoperiod interaction. Volk and Bugbee (1991) mathematically reworked the equations of Cao and Moss. Masle *et al.* (1989b) examined the effects of vernalization and photoperiod. Miglietta (1991a) predicted leaf appearance on an ontogenetic decline in the rate of leaf appearance and incorporated photoperiod effects (Miglietta, 1991b). McMaster and Wilhelm (1995) tested these equations on field data for winter and spring wheat and found that no equation adequately predicted the phyllochron for all wheat cultivars across the wide range of conditions and cultural practices represented in the field data sets. Most equations predicted spring wheat phyllochrons better than winter wheat. Based on multiple criteria, the Baker *et al.* and Kirby and Perry approach seemed

best. Other tests of some of these equations with different data sets found similar results (Bindi *et al.*, 1995; Kirby, 1995), and Kirby (1995) proposed a new equation based on day length and acclimation to temperature shortly after seedling emergence.

It is not known what mechanism(s) determines the phyllochron and whether the phytochrome system is involved (Cao and Moss, 1989a,b,c; Porter and Delecolle, 1988). Although Skinner and Simmons (1993) found no effect of FR on the phyllochron of barley, Barnes and Bugbee (1991) did show that as phytochrome photorequilibrium decreases (i.e., the R/FR ratio decreases), the phyllochron increases. The correlation reported by Baker *et al.* (1980) between change in day length and phyllochron corresponds with changes in R/FR ratio as photoperiod changes in the field.

The maximum size of successive leaf blades on a culm increases (Gallagher, 1979; Hay and Wilson, 1982; Kirby, 1993; Rawson *et al.*, 1983; Skinner and Simmons, 1993; Trought and Drew, 1980), with the exception of the flag leaf, which typically is smaller than the penultimate leaf. A linear blade elongation rate with GDD has been observed (Gallagher *et al.*, 1979; Hay and Wilson, 1982; Kirby *et al.*, 1985b). Growth of the first two leaves on the main stem is strongly dependent on seed reserves and aleurone area. Subsequent seedling development is controlled by size of the first two leaves (Peterson *et al.*, 1989). Interestingly, even with adequate water and nutrients, rooting volume can affect leaf size, but not the phyllochron (Peterson *et al.*, 1984). There appears to be a negative relationship between soil strength and leaf expansion rates (Masle and Passioura, 1987). The final number of leaves produced differs depending on the culm, with main stems producing the most leaves and a positive relationship between culm age and the number of leaves (Stern and Kirby, 1979). Stresses shorten the life span of leaves, with N being especially critical in maintaining maximum life span (Belford, 1981; Trought and Drew, 1980).

The coleoptile leaf is important in seedling emergence, in part because it protects the shoot as it pushes through the soil. Coleoptile length limits the planting depth, below which emergence is drastically reduced (Chastain *et al.*, 1995; Fedotov *et al.*, 1990; Kirby, 1993; Whan, 1976). Coleoptile length will vary greatly among cultivars and increases with deeper sowing depths (Sharma, 1990). Semidwarf wheats have shorter coleoptiles than wheat varieties without the *Rht* genes.

Stresses shorten the life span of leaves, with N being especially critical in maintaining maximum life span (Belford, 1981; Trought and Drew, 1980).

4. Tiller Primordium Elongation and Abortion

Tiller bud differentiation and extension (and thus tiller appearance) normally ends shortly after spike development starts and well before jointing (Baker and Gallagher, 1983b; Gallagher and Biscoe, 1978; Herzog, 1986; Jewiss, 1972; Kir-

by, 1985; Rawson, 1971a). However, other work suggests that tillering may not stop at a specific growth stage and, rather, that environmental factors interact with genetic factors causing variation in tiller appearance cessation (Darwinkel, 1978; Kirby, 1985; Longnecker *et al.*, 1993).

Tillering varies greatly among cultivars, with semidwarf genotypes (i.e., those having *Rht* genes) having greater tillering rates than normal genotypes (Allan, 1989; Borrell *et al.*, 1991; Fraser *et al.*, 1982; Herzog, 1986). Richards (1988) reported that the recessive gene, *Tin*, inhibits tillering in wheat.

For nonstressed conditions, tiller appearance is orderly and predictable, with specific tillers appearing only during specific windows of time (Baker and Gallagher, 1983a; Engledow and Ramiah, 1930; Hay and Kirby, 1991; Krenzer *et al.*, 1991; Masle, 1985; Rickman *et al.*, 1983). For tall fescue, cessation of cell division in the leaf sheath was associated with the initiation of cell division and elongation of the associated tiller (Skinner and Nelson, 1995). Tiller buds that do not emerge may continue to slowly grow at least until the main stem reaches anthesis (Williams, 1975). A common approach has been to view tillering over calendar or thermal time as a function of some treatment (Maas *et al.*, 1994; Miyasaka and Grunes, 1990; Sojka *et al.*, 1975). A positive relationship is found between temperature and when the window of appearance occurs. An important refinement in this approach is to base tiller appearance on leaf production, or the phyllochron. For example, Table 1 gives the times specific tillers appear in the simulation models SHOOTGRO and SPIEGRO based on the main stem Haun growth stage (McMaster *et al.*, 1991, 1992a; Wilhelm *et al.*, 1993). Table 1 deviates slightly from the common assumption that a tiller will appear when its subtending leaf and two subsequent leaves are fully expanded (Friend, 1965b; Harrell *et al.*, 1993; Kirby, 1993; Kirby *et al.*, 1985a; Masle-Maynard, 1981b), and the results in Table 1 are also supported somewhat by Longnecker *et al.* (1993). Rickman *et al.* (1985b) reported that light intensity did not affect the relationship of tiller appearance to MS

Haun growth stage. Maas *et al.* (1994) showed that salinity could delay the window of time that certain tillers appeared. Longnecker *et al.* (1993) show that N can delay tiller appearance slightly, but this is related to delayed leaf appearance. It is likely that any delay in the window of tiller appearance as influenced by nutrients is due to slower growth rates, resulting in a longer duration for tiller emergence from the axil of the associated leaf rather than an actual change in the window of appearance.

Often, physical and spatial constraints are ignored in wheat developmental morphology (Langer, 1979; Williams and Langer, 1975; Williams and Metcalf, 1975). For instance, the tiller bud is tightly contained in a cavity, and Williams and Langer (1975) view the "escape" from the cavity to be a critical event in a tiller appearing. Allometric constraints can also exist.

Not all culms produce harvestable spikes (e.g., Auld *et al.*, 1983; Darwinkel, 1978; Fraser *et al.*, 1982; Maas *et al.*, 1994, 1996; Roy and Gallagher, 1985; Shanahan, 1982; Watson *et al.*, 1963). Spatial arrangement of plants has little impact on the culm number per unit area (Auld *et al.*, 1983), although clearly plant density does have impact (Bremner, 1969; Darwinkel, 1978; Simons, 1982).

Most tiller abortion normally begins when tiller appearance stops, and tiller abortion typically ends just before anthesis (Gallagher and Biscoe, 1978). Tiller abortion particularly increases shortly after internode elongation and the terminal spikelet stage (Hay, 1986).

Most culms present at anthesis that have not begun aborting produce a spike. Aborting culms often can first be detected by noting the loss of chlorophyll from the youngest leaf that is emerging, whereas the penultimate and other leaves show no readily discernible loss of chlorophyll (observed by B. Klepper and R. Rickman, unpublished results, and verified by G. S. McMaster for other conditions).

Quantitative relationships are not well developed for determining which tillers will survive or produce spikes. The culms on a plant are integrated so that at least some "cooperation" exists (Alaoui *et al.*, 1992; Langer, 1979; Thorne and Wood, 1987b), and in at least some instances, tillers never become completely independent from the main stem (Rawson and Hofstra, 1969). However, the clear negative relationship between stand density and tiller number per plant (Bremner, 1969; Darwinkel, 1978; Simons, 1982) demonstrates that there is also competition between tillers for normally limiting resources. Despite the interplay between cooperation and competition, a few general qualitative patterns are apparent. First, tillers that have not produced three or four leaves by jointing, which is when the first nodal roots are produced on the tiller, do not produce a spike (Klepper *et al.*, 1984; Masle, 1985; Masle-Maynard, 1981b; McMaster *et al.*, 1991; Rickman *et al.*, 1985a; Wilhelm *et al.*, 1993). Second, younger/smaller tillers will senesce before older/larger culms (Bremner, 1969; Darwinkel, 1978, 1980; Engledow and Ramiah, 1930; Masle, 1985; Masle-Maynard, 1981a; Palfi and Dezsi, 1960; Shanahan, 1982; Thorne and Wood, 1988), although Thorne (1962) reported in-

Table 1
Relationship between Main Stem (MS) Development
and Culm Appearance^a

MS Haun	Culm class	Culms that appear
0.0	1	MS
1.9	2	T0
2.7	3	T1
3.3	4	T2, T00
4.0	5	T3, T10, T01
5.0	6	T4, T20, T02, T11, T100, T010, T000, T30

^a Culm naming scheme is after Klepper *et al.* (1983a). Adapted from McMaster *et al.* (1991).

stances in which older tillers died before younger tillers. Third, for tillers of the same age or size, higher-order tillers will senesce before lower-order tillers. Walter (Alaoui *et al.*, 1992; Belford, 1981; Christen *et al.*, 1995; Davidson and Chevallier, 1987; Krenzer *et al.*, 1991; Langer, 1979; Masle, 1985; McMaster *et al.*, 1994; Trought and Drew, 1980), salinity (Francois *et al.*, 1994; Maas and Poss, 1989; Maas *et al.*, 1994), nutrients (Blacklow and Incoll, 1981; Bremner, 1969; Masle, 1985; Power and Alessi, 1978), light (Langer, 1979; Masle, 1985; McMaster *et al.*, 1987; Thorne and Wood, 1987a; Willey and Holliday, 1971), and high temperatures (Cannell, 1969; Rawson, 1971a; Thorne and Wood, 1987a) all can affect tiller survival. Biotic variables and management practices, such as planting density, depth, and date, surface residue cover, and tillage, affect tiller survival primarily by the effect on abiotic factors.

The coleoptilar tiller seems anomalous to the other culms both physiologically and developmentally (Aggarwal and Sinha, 1984; Bingham, 1967; Brocklehurst *et al.*, 1978; Cannell, 1969; Fletcher and Dale, 1977; Hucl and Baker, 1989; Johnson and Moss, 1976; Kirby *et al.*, 1985b; Krenzer *et al.*, 1991; Longnecker *et al.*, 1993; Maas *et al.*, 1994; Oosterhuis and Cartwright, 1983; Peterson *et al.*, 1982; Rawson, 1971a; Richards, 1983; Smika and Greb, 1973).

Semidwarfing genes significantly reduce culm height from the original standard, or tall, cultivars. For five Mexican and one Australian cultivars, the taller the cultivar the greater the internode lengths, and all cultivars had at least four or five internodes that elongated (Rawson and Evans, 1971). Assimilate for initial tiller bud growth comes from the leaf above on the parent culm (Fletcher and Dale, 1977). The role of the phytochrome system on tiller appearance and extension has been discussed in a number of studies (e.g., Casal, 1988; Kasperbauer and Karlen, 1986; Skinner and Simmons, 1993). Vernalization increases stem length without modifying the number of nodes (Blondon and Morris, 1985). Clearly, vernalization and photoperiod influence internode elongation (Chinoy and Nanda, 1951).

5. Switch from Vegetative to Reproductive Primordium Initiation

The switch from the vegetative to reproductive phase occurs at single ridge if viewing a dissected apex, or at jointing if using external morphological characteristics.

The transition from vegetative to reproductive development varies in duration among cultivars. Semidwarf wheat cultivars derived from Norin 10 tend to have a longer transition period and produce many more single ridges than standard wheats (Fisher, 1973). Inflorescence initiation seems to occur earlier in dwarf lines (Bush and Evans, 1988), but Brooking and Kirby (1981) concluded that the Norin 10 semidwarfing genes *Gai/Rht2* do not result in consistent differences in shoot apex morphogenesis, and much of the confusion may be due to not using isolines (Gale and Youssefian, 1985).

The transition from vegetative to reproductive development can be influenced by at least four signals: vernalization, photoperiod, in some cases short day vernalization, and if many leaves have already formed (an internal signal). Not all cultivars will respond to all of these signals (Hay and Kirby, 1991).

Several studies (Baker and Gallagher, 1983a; Tottman, 1977) have tried to relate double-ridge stage to ligule or stem height above the soil surface, but these clues are very cultivar- and site-specific dependent (Yasuda, 1984). When the outline of the first internode appears, apical primordium initiation rate increases [i.e., spikelet primordium are being produced (Malvoisin, 1984)].

It is almost ubiquitously overlooked that until the transition stage, and specifically jointing, the apical meristem is below the soil surface (Hay, 1986). From jointing through maturity the apical meristem is increasingly exposed to the canopy/aerial microenvironment. Purvis (1961) learned that the shoot apex directly perceives temperature. Most developmental concepts incorporate some type of thermal time or response using temperatures above the canopy. The assumption is that there is a consistent correlation between air temperature above the canopy and apical meristem temperature. Depending on the physical location of the meristem, and the microenvironment associated with the physical location, the degree of correlation of the relationship will vary. Given the potential variability in the relationship through time, it is amazing that the growing degree-day approach works as well as it does.

Perhaps observed shifts in the phyllochron that occur in the spring near double ridge are partly related to this altered relation of the meristem to its microenvironment. Because double ridge and the start of internode elongation occur at nearly the same time, the meristem is rapidly approaching the soil surface when the shift occurs. The variable shift (increase and decrease) reported by Hay and Delecolle (1989) could be due to the highly variable relationship between air and soil surface temperature, depending on the specific conditions at the time (particularly soil water content, residue cover, and tillage practices).

Another ramification of using canopy air temperature as representative of apical meristem temperature can be misinterpreting the effects of factors on various developmental processes. This was alluded to in the previous phenology discussion. Without monitoring the apical meristem temperature, it is very difficult to know if the plant is responding to the factor or the result of the factor changing the microenvironment and apical meristem temperature, or both.

6. Spikelet Primordium Initiation

When the outline of the first internode appears, apical primordium initiation rate increases [i.e., spikelet primordium initiation begins (Malvoisin, 1984)], but double-ridge stage occurs before internode elongation (Harrell *et al.*, 1993) and after under certain conditions and cultivars (Yasuda, 1984). Spikelet formation coin-

cides with rachis internode extension in spring wheat (Holmes, 1973). Spikelet primordia are initiated acropetally (Barnard, 1955; Bonnett, 1966; Kirby, 1974). Vascular connections between the spikelet and rachis are established approximately at the time of floret initiation (Whingwiri *et al.*, 1981), and spikelet number seems to determine the amount of vascular tissue that needs to be differentiated (Evans *et al.*, 1970). Spikelets have their vascular tissue linked in parallel, whereas kernels within a spikelet tend to be linked in series (Bremner, 1972). Numerous transfer cells are found in the nodal regions where glumes, lemma, palea, and caryopsis are attached to the rachis and rachilla (Zee and O'Brien, 1971).

Some spikelet primordia, about 50% of the final number, have been initiated prior to double ridge (Baker and Gallagher, 1983a; Kirby, 1985). Other work shows contrasting results ranging from 9 to 80% of the final spikelet number initiated by double ridge (Delecalle *et al.*, 1989). The appropriate number is debatable and may be a function of cultivar variation in the number of single ridges established and the length of the transition phase from vegetative to reproductive primordium initiation (Fisher, 1973). The final maximum number of spikelets probably varies among cultivars, with a maximum of about 30 spikelets per spike (Allison and Daynard, 1976).

Spikelet primordia are initiated about two to three times faster than leaf primordia (Baker and Gallagher, 1983a,b; Delecalle *et al.*, 1989; Grieve *et al.*, 1993; Hay and Kirby, 1991; Kirby, 1974; Kirby and Appleyard, 1987; Malvoisin, 1984; Nerson *et al.*, 1990; Stern and Kirby, 1979), but the rate varies greatly among cultivars (Allison and Daynard, 1976). Several studies report that spikelet primordia initiation is a linear function of temperature/GDD (Baker and Gallagher, 1983b; Hunt and Chapleau, 1986; Kirby *et al.*, 1989; Malvoisin, 1984; Mohapatra *et al.*, 1983), although for cereal crops, certain years and cultivars may have a slight curvilinear relationship (Hunt and Chapleau, 1986). Kirby (1985) cites studies that suggest that about 0.07 spikelet primordia are formed per degree-day within a temperature range of 0 to 25°C (assuming a base temperature of 0°C). Younger tillers had faster spikelet primordium initiation rates so that the final number of spikelets per spike were similar for all culms because the higher rates compensated for the shorter duration (Hay and Kirby, 1991; Whingwiri and Stern, 1982). The vernalization response is positively related to the rate and duration of spikelet initiation (Blondon and Morris, 1985; Flood and Halloran, 1986; Halse *et al.*, 1969).

Temperature is the major variable controlling spikelet initiation rate and duration, but the role of photoperiod is much less clear. Photoperiod positively increases spikelet initiation rate (Baker and Gallagher, 1983b; Lucas, 1972; Nerson *et al.*, 1990; Rahman and Wilson, 1978), but the effect lags several days (Davidson and Christian, 1984). An increase in photoperiod likely is correlated with an increase in apex and plant temperature and may confound the response (Kirby, 1985). Later planting dates shortened the duration of spikelet primordium initiation in calendar days (Whingwiri and Stern, 1982). Low light intensity will in-

crease the duration and reduce spikelet initiation rate with a net result of fewer spikelets per spike (Davidson and Christian, 1984; Fischer, 1985; Friend, 1965a; Halse and Weir, 1970; Kemp and Whingwiri, 1980; McMaster *et al.*, 1987; Stockman *et al.*, 1983). Because low light intensity could be correlated with lower apex and plant temperature, Kirby (1985) may be correct in assuming that light, at most, has an indirect effect on spikelet initiation rates by influencing temperature. Cottrell *et al.* (1981) showed that gibberellin levels were higher in shoot apices in long days, and that higher spikelet initiation rates were greater with higher levels of gibberellin. The role of the phytochrome system has not been studied.

Nitrogen has variable effects on spikelet primordia initiation. The timing of double ridge was not affected by N (Frank and Bauer, 1982), and generally N does not increase the final number of spikelets (Langer and Liew, 1973; Nerson *et al.*, 1990; Reilly *et al.*, 1984; Single, 1964; Whingwiri and Kemp, 1980; Whingwiri and Stern, 1982; G. S. McMaster, unpublished data N, P, and Zn). N fertilizer after double ridge does not affect the final number of spikelets (Baker and Gallagher, 1983a), but this probably is because final number has already been determined.

Water stress prior to the heading growth stage does not result in spikelet death unless the whole plant dies (Morgan, 1971). Salinity was found to have no effect on initiation rate but shortened the duration of two spring wheat cultivars (Grieve *et al.*, 1993).

7. Spikelet Differentiation

Spikelet differentiation commences with the appearance of flower primordia. While flower primordia are being initiated within the spikelet, each flower primordium differentiates the various organs comprising the floret (e.g., glumes at base of spikelet, lemma, palea, stamens, and pistil). As a result, a period of time occurs in which spikelet primordia, flower primordia, and floral parts are being initiated concurrently.

With the onset of flower primordium initiation, a basic change in the morphological developmental pattern of the spike occurs and is maintained to physiological maturity. Until this point, leaf and spikelet primordia are initiated and develop acropetally. However, basal spikelets do not begin differentiation first. Florets in the mid-lower region of the mature spike (about spikelet positions 5–13) begin floret initiation first, with spikelet differentiation occurring both acropetally and basipetally from the mid-lower region. Some discrepancy exists between whether the basal (Kirby, 1974) or distal spikelets (Whingwiri and Stern, 1982) differentiate first. Some of the discrepancy is due to initiation starting in the lower mid-central region, resulting in more potential distal than proximal spikelets; thus, the most distal spikelets may start differentiating last if an even progression occurs both acropetally and basipetally. Within a spikelet, floret primordia are initiated acropetally. The MS begins floret formation before the tillers.

Stem elongation has just begun (i.e., the stem is less than 5 mm and the apex is below the soil surface) when the first florets are initiated (Baker and Gallagher, 1983a; Nicholls, 1974). This would mean that spikelets begin differentiating very shortly after double ridge, if one assumes that double ridge and the start of internode elongation are simultaneous.

Reports are consistent in the literature that floret formation begins prior to TS stage, but considerable variation in the number of floret primordia per spikelet at TS stage has been reported. For instance, Kirby (1974, 1985) found about two or three florets on spikelets near the mid-lower portion of the spike at TS stage. Whingwiri and Stern (1982) report that all spikelets on a culm have begun floret initiation before formation of the TS. They observed that most fourth florets were initiated between 1 and 8 days after TS formation, usually within 3 days. About 48% of the third florets were initiated before TS formation, 40% after the TS, and the remainder at the same time as TS. Time of sowing did not seem to greatly alter the interval between floret initiation and TS formation. With some exceptions, N supply appeared to advance floret initiation but not TS formation, although N did not affect the rate or duration of floret initiation (Langer and Hanif, 1973; Whingwiri and Stern, 1982). On later-formed tillers, fewer florets were initiated before TS formation.

Before significant floret development occurs in Norin 10 and derivatives, the glume and lemma primordia grow within a spikelet to a greater extent than in standard wheat cultivars (Fisher, 1973). Fisher attributes this difference among genetic lines to differences in apical dominance. Differences in apical dominance may account for differences in the number of floret primordia within a spikelet before stamen primordia appear, and that Norin 10 and derivatives (i.e., those with greater tillering tendency, and presumably reduced apical dominance) will produce more floret primordia before stamen primordia are initiated than standard wheats (Fisher, 1973). Williams (1966a) gives relative growth rates, volumes, weights, and lengths of various spike organs as well as the whole spike, shows that stamen and carpel volumes in successive florets within a spikelet are lower, and shows that duration of growth is shorter within successive florets; the shorter durations of successive florets lead to synchrony within the spike (Hay and Kirby, 1991).

Spikelet development rate varies considerably within the spike, with terminal spikelets, central spikelets, spikelets just above and below the central spikelets, and basal spikelets having successively decreasing developmental rates (Barnard, 1955). However, this is not an absolute pattern of spike developmental rates (Barnard, 1955). Kirby (1974) found that the difference in number of florets in spikelets differed not due to different initiation rates, but rather because the duration of initiation was shorter in non-centrally located spikelets, and Kirby and Appleyard (1987) suggest that floret initiation rate is essentially similar for all spikelets. Estimated floret initiation rates usually range from 0.02 to 0.04 florets

$^{\circ}\text{C}^{-1} \text{ day}^{-1}$ (Kirby, 1974; Kirby and Appleyard, 1987; Whingwiri and Stern, 1982), or about 25 GDD between successive florets (Williams, 1966b). Temperature, and possibly light, are the main factors influencing spikelet development rates (Friend *et al.*, 1963; Hay and Kirby, 1991; Masle *et al.*, 1989a). Temperatures above 30°C during floret formation have been reported to cause complete sterility (Owen, 1971; Saini and Aspinall, 1982).

A maximum of 8–12 flower primordia initials are present on each mid-central spikelet and about 6–8 on basal and distal spikelets, but less than half of these are fertile florets at anthesis because at least half abort or have developed insufficiently before anthesis to be fertile (Barnard, 1955; Engledow and Ramiah, 1930; Hay and Kirby, 1991; Herzog, 1986; Kirby, 1974, 1985, 1988; Kirby and Appleyard, 1987; Langer and Hanif, 1973; Siddique *et al.*, 1989; Single, 1964; Whingwiri and Stern, 1982).

Flower primordia initiation stops in the lower mid-central spikelets within the spike as the flag leaf begins emerging (Baker and Gallagher, 1983a; Kirby, 1988). It is not clear if flower primordium initiation ceases simultaneously for all culms and all spikelets on a culm.

Floret abortion begins at booting, or when the flag leaf is fully grown, and floret initiation has ceased and lasts about two phyllochrons, after which no further floret abortion occurs; abortion ends at about heading or anthesis (Kirby, 1985, 1988; Langer and Hanif, 1973; Siddique *et al.*, 1989). Predicting which florets will abort is difficult, but the literature is consistent in that at least half of the total floret initials within a spikelet will abort or develop insufficiently to be fertilized by anthesis. Whingwiri and Stern (1982) suggest that all florets initiated after the terminal spikelet is formed will not develop grain.

Floret death occurs during the period when the stem and peduncle are growing at their most rapid rate (Siddique *et al.*, 1989). The penultimate internode is at maximum growth rate and the peduncle growth rate is rapidly increasing. During this period, leaf area is slowly declining, although total photosynthetic rate may not initially be declining, particularly when spike photosynthesis is included. Kirby (1988) interprets this as support for the hypothesis that floret death is partly due to competition between the spike and stem for resources, presumably carbohydrates. One difficulty with this hypothesis is that often there are excess carbohydrates available during this phase and these carbohydrates are stored in the internode tissue, although the reserves are usually stored more closely to the period near or after anthesis (Asana and Williams, 1965; Blacklow *et al.*, 1984; Judel and Mengel, 1982; Wardlaw, 1970).

Barnard (1955) outlined the histogenesis of the spike and was led to the following conclusions. The foliage leaf, glume, lemma, palea, lodicules, and carpel are viewed as foliar appendages. Stamens, lateral spikelet primordia, and flower primordia are considered homologous with axillary vegetative shoots. Fisher (1973) agreed with this interpretation.

8. Floret Differentiation

The first glume, lemma, and palea primordia appear on spikelets near the central portion of the spike (Baker and Gallagher, 1983a; Barnard, 1955; Bonnett, 1966; Kirby, 1985; Oosterhuis, 1977). The two glumes within a spikelet differentiate first, followed by the first two lemmas on the basal florets within a spikelet. As the third lemma differentiates, the first flower primordium appears in the axil of the first lemma (Barnard, 1955). Stem elongation begins when lemma primordia first appear or slightly earlier (Kirby, 1985; Malvoisin, 1984; Tottman, 1977), but others (Masle *et al.*, 1989a; Wiegand *et al.*, 1981; Yasuda, 1984) did not find this relationship.

Within a floret, the order of differentiation is from the outside inward: lemma, stamens, palea, and pistil (Bonnett, 1966; Oosterhuis, 1977). However, Barnard (1955) indicated the order of the stamens and palea was reversed, which would result in a two-ranked order of differentiation. Awns develop on lemmas; therefore, for awned cultivars, development of the awn is associated with lemma development. Awn structures begin to elongate on the lemmas after the appearance of the stamens (Oosterhuis, 1977). Conflicting reports exist on whether awns positively (Weyhrich *et al.*, 1994) or negatively (McKenzie, 1972) impact grain yield and test weight. A floret is particularly sensitive to stresses when the subtending lemma is being initiated (Frankel, 1976).

The two lateral stamens in a floret appear first, followed by the anterior stamen and carpel (Barnard, 1955). The two lateral stamens are positioned in the keels of the palea, with the central stamen opposite the lemma on the adaxial side (Bonnett, 1966). The visible appearance of the first anther primordium on the most advanced spikelet generally coincides with the initiation of the terminal spikelet just prior to jointing (Fisher, 1973; Friend *et al.*, 1963; Williams, 1966a). Anther initials are the first part of the stamen to differentiate, with the filament forming later beneath the anther (Bonnett, 1966). The four locules form in each anther soon after the anthers are initiated (Bonnett, 1966). For some cultivars, high temperatures (24/19 and 30/25°C) can result in poor pollen development (Dawson and Wardlaw, 1989).

Fewer pollen grains are produced in wheat stamens (about 1000–3800 per anther) than in other cereal grasses, and wheat stamens are smaller than those of other cereals (de Vries, 1971). Total pollen production per wheat plant is about 450,000 as contrasted to about 4 million for *Secale cereale* L. (rye) and 18 million for *Zea mays* L. (corn; de Vries, 1971). It might be speculated that fewer pollen grains are necessary for wheat, which self-pollinates, than for rye and corn, which are cross-pollinated.

The pistil is the last floret structure to initiate (Bonnett, 1966). The order of pistil differentiation is ovary, styles, and stigma (Bonnett, 1966). The carpel of wheat

is unilocular, with one ovule. Each ovule has two plumose styles with stigma branches. Throughout development, very low concentrations of polysaccharides and reducing sugars and high concentrations of RNA and nuclear proteins are present in stigmatic branches; lipids increase during pollination and decrease during pollen growth (Rudramuniyappa and Panchaksharappa, 1974). Pollen grains and pollen tubes have high concentrations of polysaccharides, RNA, proteins, and lipids. Rudramuniyappa and Panchaksharappa (1974) infer that these macromolecular substances balance out the need for growth of the pollen tube in the stigma and style.

9. Terminal Spikelet Formation

The TS is characterized by a 90° rotation from the plane of previous spikelet initials (Fig. 6; Bonnett, 1966; Hay and Kirby, 1991). The TS is formed just prior to jointing, when the stem is about 20 mm long (Baker and Gallagher, 1983a), and the TS primordium appearance coincides with the appearance of the first stamen primordium (Fisher, 1973; Williams, 1966a). There does seem to be some variability, however, in the relationship of TS formation and other developmental events (Whingwiri and Stern, 1982). Nicholls (1974) suggested that cessation of spikelet primordium formation by the apical meristem is not correlated with any developmental stage, and that nutrient limitation is the cause for cessation. However, nitrogen had no effect on it when the TS appeared (Whingwiri and Stern, 1982). Photoperiod profoundly impacts when the TS is initiated, but this is likely cultivar dependent (Pinthus and Nerson, 1984; Rawson, 1971b). Probably, the TS stage is not strongly correlated with other developmental events. Terminal spikelet initiation occurs later on younger culms, although the range was less than about 3 days among all culms (Whingwiri and Stern, 1982). Baker and Gallagher (1983a) showed a 6-day difference among the MS and T1 culms.

The presence of the TS has led Bonnett (1966) and others to view the wheat spike as determinate, although an apical meristem does remain after the TS has differentiated (Fisher, 1973). In a practical sense, the wheat spike can be viewed as determinate because further apical meristematic activity ceases under almost all conditions.

10. Rachis Growth

Rachis internode extension coincides with spikelet formation for spring wheat (Holmes, 1973). Spike growth is very slow in the early stages of development and rapid elongation starts when the flag leaf ligule is just visible (Krumm *et al.*, 1990). It is unclear when rachis elongation ceases, but it is certainly before anthesis (McMaster *et al.*, 1992b). Spike length increase seems fairly linear over time (Mishra

11. Peduncle Growth

Peduncle elongation occurs during booting into anthesis. Depending on conditions and cultivars, elongation and dry weight increase ends between anthesis and about 2 weeks post anthesis (e.g., Asana and Williams, 1965; Davidson and Chevalier, 1992; Judel and Mengel, 1982; McMaster *et al.*, 1992b; Rawson and Evans, 1971; Spiertz, 1974; Wardlaw, 1970). Internodes other than the peduncle can sharply decrease weight at anthesis, especially at higher temperatures (Spiertz, 1974). Stem dry weight (presumably including the peduncle) increased faster than spike dry weight for the first 10 days following anthesis (Wardlaw, 1970). N has little effect on the qualitative and quantitative changes in soluble culm carbohydrates (Blacklow *et al.*, 1984), but light intensity is positively correlated with stem weight (Spiertz, 1977).

Peduncle growth rate and other internode growth rates were given by Kirby (1988). Reported peduncle lengths range from about 150 to 350 mm for seven cultivars (McMaster *et al.*, 1992a; Rawson and Evans, 1971).

12. Chaff Growth

Chaff normally is composed of glumes, paleas, lemmas, awns, rachillas, and rachis. Asana and Williams (1965) found that chaff weight did not increase after 12 days post anthesis (about 385 GDD). Chaff dry weight at harvest can range from 6 to 54% of total spike weight, depending on cultivars and conditions (Asana and Williams, 1965; Bingham, 1967; McMaster *et al.*, 1994; Miller, 1939). For cultivated spikes, lower temperatures result in a lower proportion of the spike weight represented by nongrain fractions (Donovan *et al.*, 1983). Irrigation significantly increases glume weight, but N has no significant effect (Bingham, 1967). There is a positive correlation between kernel and chaff weight (G. S. McMaster, unpublished data). For "Gabo", a cultivar with a short tip awn in the distal three or four spikelets, awn weight per spike ranged from about 2 to 22 mg per spike and was strongly influenced by N (Single, 1964).

13. Anthesis

The two lodicules at the base of the ovary are placed against the lemma and at the edges of the palea (Bonnett, 1966). The thick bases of the lodicules swell to twice their size, probably due to sugar influx causing osmotic swelling, forcing the palea and lemma to open and allowing anther extrusion (Fig. 6; Bonnett, 1966; Craig and O'Brien, 1975; Percival, 1921). Stamen filaments can elongate to three times their original length within 3 min (de Vries, 1971), causing anther exertion. Approximately 20 min following the swelling of the lodicules, the palea and lemma close and anthesis is complete. Although the opportunity for cross-pollination

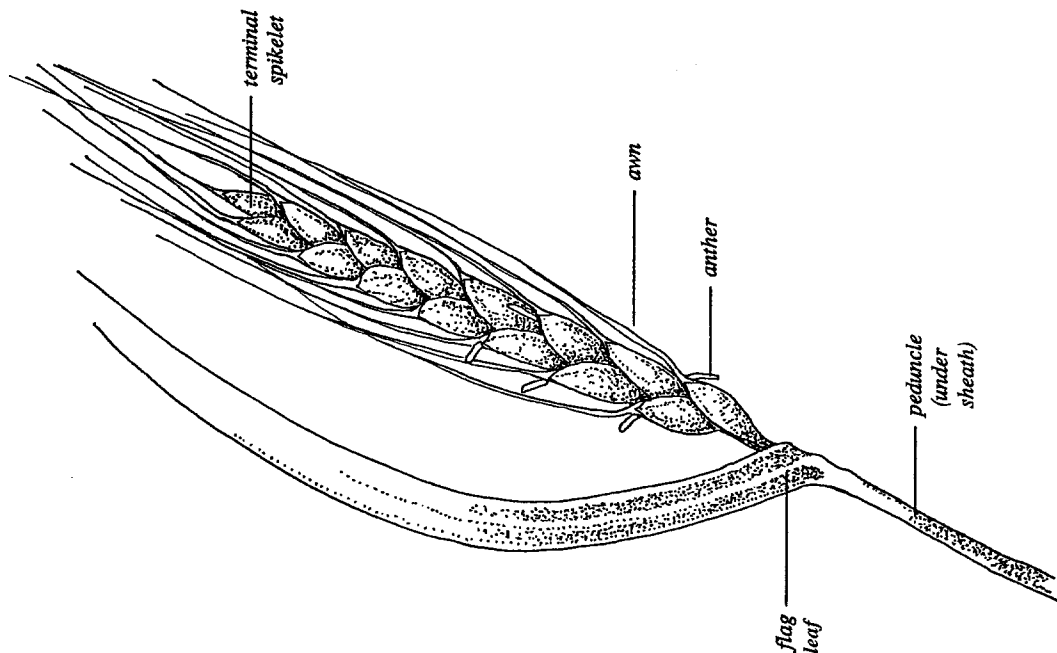


Figure 6. Drawing of a wheat spike at anthesis growth stage.

and Mohapatra, 1987). The MS ear length grows at a maximum rate of 0.73 mm per degree-day and during the linear phase has a rate of 0.51 mm per degree-day (Kirby, 1988), although cultivar differences and varying conditions will result in different rates. Spike lengths and weights vary considerably among cultivars and conditions, with N stress reducing lengths and weights (Large, 1954; Singh and Singh, 1985; G. S. McMaster, unpublished data).

occurs during this time, over 96% of the wheat flowers are self-pollinated (Martin *et al.*, 1976). Pollen viability is maintained for up to 30 min under optimal conditions (de Vries, 1971), after which the pollen grains become desiccated. Pollen germinates within 1 min of reaching the stigma (Chandra and Bhatnagar, 1974), with usually only one grain germinating on a stigma branch (Rudramuniyappa and Pan-chaksharappa, 1974). The pollen tube enters the embryo sac from 30 to 60 min after germination (Lange and Wojciechowska, 1976), and Jensen (1918) observed that fertilization occurs between 32 and 40 hr after pollination.

Fertilization is kleistogamous, meaning pollination occurs prior to the phenological growth stage called anthesis (Herzog, 1986; Martin *et al.*, 1976). Ovule fertilization begins in basal florets within spikelets in the central portion of the spike and proceeds simultaneously acropetally and basipetally along the rachis and acropetally within the spikelet (Bonnert, 1966; Oosterhuis, 1977; Rawson and Evans, 1970). All ovules within a spike are fertilized within a short span of time, usually within about 3 days (Evans *et al.*, 1972; Rawson and Evans, 1970; Simons and Crookston, 1979). Sterilization of basal spikelets in central florets did not affect the onset of anthesis of other florets (Rawson and Evans, 1970). Only about 80% of the fertile florets set grain (Gallagher and Biscoe, 1978).

Much discussion and anecdotal evidence exists for the importance of water in pollination and successful grain set; however few detailed studies examining plant water potential during pollination and wheat pollination or grain set have been published to my knowledge. Higher N seems to increase the number of fertile florets at the time of fertilization (Langer and Liew, 1973; Single, 1964), although it is unclear how this affects grain set. Single (1964) found little influence of N on grain set, but Langer and Liew (1973), Whingwiri and Kemp (1980), and others have found more kernels per spikelet under high N conditions.

A parabolic pattern of number of kernels per spikelet within a spike is observed (Grieve *et al.*, 1992; Lesch *et al.*, 1972). Maximum number of kernels per spikelet occurred in the range of 25–50% up the rachis (Herzog, 1986). Whingwiri and Stern (1982) found that only florets that initiated prior to TS formation formed grain. Three hypotheses have been advanced to explain why florets fail to develop into kernels: (i) an inadequate supply of mineral nutrients, water, and carbohydrates; (ii) hormonal imbalances; and (iii) further development is dependent on vascular development that is a function of the interaction between sucrose and hormones such as auxin. Indirect evidence exists to support all three hypotheses (Whingwiri and Stern, 1982).

14. Kernel Growth

Individual kernel growth follows a sigmoidal pattern regardless of location within the spike, among spikes, among cultivars, or any typical set of biotic or abiotic factors (e.g., Barlow *et al.*, 1980; Darroch and Baker, 1995; Gebeyehou *et al.*,

1982; Green *et al.*, 1985; Herzog, 1986; Pinthus, 1963; Rawson and Evans, 1971; Slafer and Savin, 1994). The sigmoidal curve is frequently divided into three phases: the lag or cell division phase, the linear or grain-filling phase, and the asymptotic or maturation phase (Herzog, 1986). Precise determination of each phase is difficult, and the phases are most profitably viewed heuristically. The lag phase is dominated by cell division (Evers, 1970; Jennings and Morton, 1963). The duration of the lag phase is about 20–30% of the total grain-filling period, if one assumes that the grain-filling period ends when the curve approaches the asymptote (very difficult to precisely determine; Gebeyehou *et al.*, 1982; Herzog, 1986). During the lag phase, both the amount of water and seed water potential increase (Barlow *et al.*, 1980). The linear phase is the period of rapid cell growth and constitutes about 50–70% of the total grain-filling period. Herzog (1986) states that kernel growth in the linear phase is mostly caused by starch synthesis in the amyloplasts of endosperm cells. Brocklehurst (1977) suggests that assimilate supply regulates the number of endosperm cells formed, and that the rate of dry weight accumulation is primarily governed by the number of endosperm cells present. Radley (1978) found that endosperm and aleurone cell numbers increased when other kernels were removed, resulting in increased grain volume.

The end of kernel growth is normally considered to be the point of maximum dry weight. Either because the data are often variable or because sampling is not frequent enough, it is very difficult to determine the point of maximum dry weight. End of kernel growth is often determined mathematically or visually as grain weight “stops increasing.”

When considering the sigmoidal pattern of kernel growth, the two important biological variables are the duration of the grain-filling period and the instantaneous rate of grain filling. Kernel weight is commonly assumed to begin increasing at the onset of anthesis. However, Wardlaw (1970), citing others, indicated that significant dry weight gain does not begin until 6 days after anthesis. Although the error is slight, there are two inaccuracies in this assumption. The first is that fertilization occurs just prior to anthesis, where anthesis is defined as the period when stamens emerge from the floret (see Seed Ontogeny section). The second inaccuracy is that fertilization throughout the spike is not simultaneous. The duration of anthesis is normally about 3–4 days (see Phenology and Anthesis sections). It appears, and is almost universally assumed, that synergamy follows the anthesis pattern and that the time lag between fertilization and anthesis of a floret is constant regardless of floret location.

a. Seed Ontogeny

Knowledge of the ontogeny of the wheat seed is important in providing a developmental framework within which physiological processes can be understood. In discussing the ontogeny of the seed, two aspects are of primary importance: embryogeny and endosperm development. The triploid endosperm nucleus is formed

2–3 hr after pollination, whereas the diploid zygote forms some hours later (Herzog, 1986, citing many references). Zygote mitotic division begins later than endosperm mitotic division (more than 12 hr after pollination compared to 6–8 hr, respectively; Herzog, 1986; Morrison, 1955), but embryo development is completed prior to endosperm maturity (Martin *et al.*, 1976). Initial endosperm development is free-nuclear (coenocytic) mitotic divisions of varying duration (Frazier and Appalanaidu, 1965; Morrison, 1955). Endosperm cell walls begin forming about 3 days after pollination—when about several hundred nuclei have formed and 8–10 cells are present in the embryo (Deshpande and Raju, 1979; Frazier and Appalanaidu, 1965; Morrison, 1955). Endosperm development continues to proceed faster than embryo development, which is typical in flowering plants (Herzog, 1986; Lersten, 1987; Noda *et al.*, 1993). The first phase of kernel growth was previously mentioned as a time of cell division. During this period, endosperm and embryo cell division is rapid, but little growth (either in size or in weight) is occurring (Martin *et al.*, 1976). Endosperm cell division ceases after the first 10–20 days of the grain-filling period, after about 100,000 endosperm cells are present (Briarty *et al.*, 1979; Evers, 1970; Jennings and Morton, 1963; Sandstedt, 1946; Wardlaw, 1970). Little endosperm cell division occurs after this period in late grain filling. Cell number of the testa-pericarp remains constant from 5 to 40 days after flowering (Jennings and Morton, 1963). It is unclear if this suggests that maximum potential size of the seed coat is determined shortly after anthesis.

Once endosperm cell division has almost ceased, significant cell growth begins. Cells typically expand about 10-fold their initial cell size (Briarty *et al.*, 1979), with cell expansion continuing until shortly before maturity. Cell growth in dry weight terms is primarily from conversion of translocated sucrose to starches and accumulation of nitrogenous organic compounds such as protein bodies (present 10 days after anthesis; Evers, 1970) that pass through the vascular bundle that extends from the base to apex of the seed through the pericarp at the base of and parallel to the crease (Frazier and Appalanaidu, 1965). Martin *et al.* (1976) state that starch grains and proteins fill the endosperm region in a centripetal manner (i.e., outer periphery cells first). The number of starch granules is greater in large than in small kernels, and regardless of kernel size, granules less than 10 μm in diameter (B-type granules) contribute more than one-third of the total starch weight (Brocklehurst and Evers, 1977).

The final kernel is composed of about 2.5% embryo tissue, 10% pericarp, 4% aleurone, and 85% starchy endosperm (Bradbury *et al.*, 1956; Lersten, 1987; Martin *et al.*, 1976). Engledow and Ramiah (1930) described major stages of grain formation, and Noda *et al.* (1993) propose a reclassification of the developmental stages of kernels.

For spring wheat, the main vascular bundle of the caryopsis begins differentiation shortly after anthesis and is completed about the same time that caryopsis elongation ends (approximately 30% into grain filling, when cell division ends;

Lingle and Chevalier, 1985). The sieve tubes of the main bundle appear to remain functional until physiological maturity (Lingle and Chevalier, 1985).

After maturity, cultivars with red kernels normally are more resistant to sprouting than those with white kernels, which presumably is due to germination inhibitors present in the seed coat (Miyamoto *et al.*, 1961).

A complete bibliography of grass and wheat caryopsis anatomy and fine structure is available (Lersten, 1987; Rost and Lersten, 1973), and Lersten (1987) gives more detail on endosperm and embryo development.

b. Kernel Growth within a Spikelet

Regardless of kernel location within or among spikes, seed embryogeny and the sigmoidal pattern of growth is the same. However, the specific pattern of kernel growth, and the onset and completion dates, does vary depending on location. Within a spikelet, kernels develop and grow in an acropetal pattern (Bonnert, 1966; Kirby, 1974; Oosterhuis, 1977; Whingwiri and Stern, 1982). Therefore, the onset of kernel growth is progressively delayed for kernels closer to the apex of the rachilla. It is commonly assumed that basal kernels within a spikelet complete growth before apical kernels, but the data are not definitive on this and the lag time has not been adequately quantified. Simmons and Crookston (1979) reported for three spring wheat cultivars that all kernels within a spikelet reached maturity at about the same time. The lack of a precise determination, and definition, of kernel maturity contributes to the confusion on this point.

Final kernel weight varies considerably depending on abiotic and biotic factors, but a clear trend is that kernel weight decreases acropetally within a spikelet (Bremner, 1972; Rawson and Evans, 1970), and kernel weight is positively correlated with volume of the floret cavity (Millet, 1986). Conflicting reports exist on whether the first or second kernel from the base of the rachilla has greater growth rates and final dry weight (Bremner, 1972; Rawson and Evans, 1970). Aside from possible errors in identification, this pattern may be related to cultivar differences, but more likely seems to be a function of whether stresses were present during grain filling. Bremner (1972) hypothesized that the second kernel had greater potential growth rate than the basal kernel but was affected more when resources were limiting. I have noticed that studies reporting that the second kernel tends to have slightly greater final kernel weight were usually conducted in growth chambers or greenhouses in which water and nutrient supply was plentiful. In studies in which stresses were likely to be present, particularly field studies, the first kernel tends to have the greatest final weight.

c. Kernel Growth among Spikelets

Kernel growth rates, duration, and final weights vary depending on location within the spike, even under favorable conditions for grain filling (Grieve *et al.*, 1992; Lesch *et al.*, 1972; Mishra and Mohapatra, 1987; Slafer and Savin, 1994).

As stresses increase, the variation among kernels within the spike increases. Several studies (Bremner, 1972; Rawson and Evans, 1970) suggest that the variation among kernels is based on different maximum growth rate potentials and on different durations of grain filling (due primarily to different fertilization times); these two factors are accentuated by physiological conditions under which stresses result in lower final kernel dry weights. These factors imply that all kernels do not have equal sink strengths. Kernel sink strength within a spike seems to follow the fertilization pattern, although many factors determine sink strength.

d. Duration of Kernel Growth within a Spike

The duration of grain filling among kernels within the spike has not been definitively quantified; it is unclear whether all kernels end grain filling simultaneously or whether the stagger in kernel maturity follows the fertilization pattern, but that the stagger in maturity covers a shorter time span than the fertilization pattern. Visual observations of greenness indicate that kernels do not mature simultaneously. For example, kernels in the terminal spikelet seem to be among the first to lose chlorophyll, which is usually an indicator of maturity (Hanft and Wych, 1982; G. S. McMaster, personal observation), and physiological maturity occurred first in kernels in the apical spikelets (about 3 days earlier) and simultaneously on kernels in central and basal spikelets for eight different cultivars of spring wheat (Hanft and Wych, 1982).

e. Kernel Growth among Spikes

The relationships discussed previously for kernel growth within a spike apply to all spikes. The main differences between kernel growth on main stems and tillers are that kernel growth rates, grain-filling duration, and final kernel weights are less on tillers (Hucl and Baker, 1989; Shanahan *et al.*, 1984; Zwer *et al.*, 1995). The onset of fertilization is delayed as tiller age and size is decreased.

The proportion of total yield contributed by each culm is not the same for all culms (McMaster *et al.*, 1994; Power and Alessi, 1978). Culm age and size are both positively related to spike grain weight (Darwinkel, 1980; Hucl and Baker, 1989; Kirby *et al.*, 1985b; Phadnawis and Saini, 1986; Saini and Nanda, 1986; Shanahan, 1982; Thorne and Wood, 1988). Usually, if tillers are of the same age, higher-order tillers will have less grain weight.

f. Cultivar Variations in Kernel Growth

Kernel growth is significantly different among cultivars (e.g., Bruckner and Froberg, 1987; Darroch and Baker, 1995; Housely *et al.*, 1982; van Sanford, 1985; Vos, 1985), and the presence of semidwarfing genes reduces kernel size (Pinthus and Levy, 1983). All growth parameters (duration of grain filling, growth rates, and final kernel weight) vary among cultivars. Although these growth parameters differ among cultivars, the pattern of individual kernel ontogeny and growth normally does not differ significantly among cultivars.

g. Temperature Effects on Kernel Growth

Temperature has a major effect on both the duration and the rate of grain filling. Each of these effects and their net results will be discussed in detail, but the general relationship is that as temperature increases the duration decreases and growth rates increase with a net effect of lower final kernel weight at higher temperatures (e.g., Bhullar and Jenner, 1983; Herzog, 1986; Sayed and Ghandorah, 1984; Sofield *et al.*, 1974; Spiertz and Vos, 1985; Vos, 1985; Wardlaw *et al.*, 1989).

The duration of grain filling is highly variable, depending in part on cultivar and environmental conditions, particularly temperature (Darroch and Baker, 1995; Ford *et al.*, 1976; Midmore *et al.*, 1982; Wiegand and Cuellar, 1981). Wiegand and Cuellar (1981) observed a decrease of 3.1 days in duration for every °C increase in temperature. If the GDD approach is used, a nonlinear relationship with temperature is found; as temperature increases, the accumulated GDD for grain-filling duration decreases (Al-Khatib and Paulsen, 1984; Asana and Williams, 1965; Marcellos and Single, 1972; Spiertz and Vos, 1985; Vos, 1985). Some uncertainty in the qualitative pattern with temperature is due to an insufficient number of temperature treatments to adequately describe a nonlinear curve.

Temperature clearly has a positive influence on kernel growth rates (Al-Khatib and Paulsen, 1984; Rawson and Evans, 1970; Wiegand and Cuellar, 1981). Most studies cite some type of linear increase in kernel dry weight with increasing temperature, although the relationship probably is not linear over the whole temperature range. Unstated assumptions in the literature include kernel growth rate responses do not vary depending on the phase of grain filling or location as in a spike.

Above a threshold temperature, final kernel weights decrease (Wiegand and Cuellar, 1981). Both high and low temperatures will inhibit starch synthetase (Jenner, 1968). Some studies show an optimal maximum grain weight for temperatures between 15 and 20°C (Chowdhury and Wardlaw, 1978; Feyerherm and Paulsen, 1981; Fischer, 1985; Herzog, 1986, cites many references; Kolderup, 1979; Sofield *et al.*, 1977b; Wardlaw *et al.*, 1989; Wiegand and Cuellar, 1981).

h. N Effects on Kernel Growth

Other factors beside temperature affect the rate and duration of kernel growth, with N and water being two frequently studied factors (Blacklow and Incoll, 1981; Herzog, 1986; Simmons and Moss, 1978a; Simmons and Moss, 1978b). Nitrogen accumulation in the kernel also follows a sigmoidal pattern, and the parameters of the curve vary among cultivars (Campbell *et al.*, 1990; Herzog, 1986; Sofield *et al.*, 1977b; Vos, 1985). Comparing the first three basal kernels in a spikelet, limited N seems to affect the third kernel most (Whingwiri and Stern, 1982). The N concentration in a kernel ranges typically between 2 and 5% during grain filling (Anderson *et al.*, 1991; Bhullar and Jenner, 1983; Griewe *et al.*, 1981; Herzog, 1986; Smith *et al.*, 1983), with 25–50% of the grain N resulting from N uptake by plants during grain growth [Austin *et al.*, 1977a; Griewe *et al.*, 1981; Heitholt *et al.*, 1990 (less than 10%); Spiertz and de Vos, 1983]. Mobilization of plant N oc-

curs from all plant parts, with leaf, glume, stem, and root fractions contributing about 40, 23, 23, and 16%, respectively (Simpson *et al.*, 1983). Temperature affects N and dry matter accumulation patterns in a similar manner (Bhullar and Jenner, 1983; Herzog, 1986; Spiertz and Vos, 1985).

Nitrogen may (Bauer *et al.*, 1985; Blacklow and Incoll, 1981) or may not (Bingham, 1967) affect the timing and duration of grain growth. Certainly, deficient N reduces leaf area duration during the period from anthesis to maturity, and it is likely N may indirectly effect grain-filling duration by altering senescence of the plant. Other nutrients besides N are obviously important in kernel growth, but have received much less attention.

i. Water Effects on Kernel Growth

Water availability has many effects on the rate and duration of grain growth such as carbon assimilation, nutrient uptake by roots, and cell division and expansion. Water availability interacts with N to decrease the mobilization of amino acids (Aggarwal and Sinha, 1984) and the interaction of water and N can result in varying effects on grain yield (Christen *et al.*, 1995; Grieve *et al.*, 1981; Mogensen and Talukder, 1987; Palta *et al.*, 1994; Palfi and Dezsi, 1960; Spiertz and de Vos, 1983). Clearly, water availability is strongly correlated with kernel growth and yield (Bingham, 1967; Brocklehurst *et al.*, 1978; Brooks *et al.*, 1982; Fischer, 1973; Fischer and Maurer, 1978; Gallagher *et al.*, 1976; Johnson and Moss, 1976; Richards, 1983), although some studies suggest that grain water potential is largely independent from the rest of the plant (Barlow *et al.*, 1980; Brooks *et al.*, 1982). It is almost certain that the duration of grain filling is shortened by water stress (Angus and Moncur, 1977; Bauer *et al.*, 1985; Bingham, 1967 (found no effect); Brooks *et al.*, 1982; Frank *et al.*, 1987; McMaster and Smika, 1988; Mogensen and Talukder, 1987; Nuttonson, 1948; Sionit *et al.*, 1980], but the effect may be indirect because plant temperature is increased. Water stress does not seem to have as great an effect on growth rates (Mogensen and Talukder, 1987). Water deficits did not affect the number of endosperm cells (Brooks *et al.*, 1982), but presumably cell expansion was affected.

j. Light Effects on Kernel Growth

Temperature accounts for 75–97% of the variation in duration of the grain-filling phase, with photoperiod having no influence (Marcellos and Single, 1971). I can find no reports that photoperiod affects the duration of grain filling. Sofield *et al.* (1977a) reported no effect of illuminance on the duration of the linear growth phase. Shading and low light intensity reduce the number and weight of kernels per spikelet and number of spikelets per spike (e.g., Evans, 1978; Fischer, 1985; Friend, 1965a; Friend *et al.*, 1963; Kemp and Whingwiri, 1980; McMaster *et al.*, 1987; Sofield *et al.*, 1974; Stockman *et al.*, 1983). Light affects grain filling primarily by its effect on the production of carbohydrates and N accumulation (Her-

zog, 1986), although Millet and Pinthus (1984) showed that the size of the floret cavity and the transmission of light through floret bracts are two other factors that control grain growth.

k. Vascular Connections within the Spike

Several studies have examined whether translocation from sources to the sink limits grain filling. Flow of sucrose is restricted by the capacity of at least one of the processes involved with transporting sugar into the grain (Jenner and Rathjen, 1972). The rate of grain filling is not related to the number of sieve tubes of the main vascular bundle of spring wheat kernels (Lingle and Chevalier, 1985). Evans *et al.* (1970) suggested that wild diploid progenitors of wheat may have had spikes that were largely self-supporting for their assimilates. In hexaploid *Triticum aestivum*, however, this is not the case. In addressing whether the stem in *T. aestivum* has the capacity to transport sufficient assimilates to meet spike demand (as this is a recent result of selection), Evans *et al.* (1970) examined the number of vascular bundles and phloem cross-sectional area among different evolutionary lines. They showed a positive relationship between phloem area and maximum translocation rate. Making a number of assumptions, Evans *et al.* (1970) concluded that the phloem present in all evolutionary lines could transport sufficient assimilates to meet spike demands. However, if this conclusion is not true, then transport limitations most likely would be found in hexaploid cultivars of recent origin. They also reported that spikelet number seemed to determine the amount of vascular tissue that needed to be differentiated.

For two spring wheat cultivars, the vascular connections in the rachilla had much smaller diameter vascular bundles connecting to the fourth and fifth kernels than the first three kernels (Simmons and Moss, 1978a). In addition, all bundles that served the fourth and fifth kernels were connected to bundles that served at least one of the first three kernels. At least some of the bundles that served the first three kernels were independently connected to the rachis. Bremner (1972) presented evidence that both spikelets and kernels within spikelets were linked both in parallel and serial, but that spikelets showed more tendency for parallel linkage and kernels within spikelets tended more toward serial linkages. This tendency might explain in part why kernels within spikelets decrease in final weight acropetally, especially when stresses increase, because resources presumably become more limiting in distal vascular regions first. This vascular system allows resources to be transported to all parts of the spikelet but also results in resources first becoming limiting in regions within the spikelet that have invested the fewest resources in development and growth—the apical florets and kernels. The greater parallel linkage among spikelets might partly account for the frequent response of basal and apical spikelets both being reduced similarly under stress conditions.

The upward velocity of assimilates through the peduncle (about 80–100 cm/hr) is twice that for movement down through the leaf sheath (Wardlaw, 1965). Re-

moving kernels slowed transfer rates upward and increased transfer down the stem. Wardlaw presented no data suggesting translocation was limiting kernel growth.

1. Sources and Sinks Present during Kernel Growth

Sources and sinks change over the course of grain filling. During early grain filling a number of sinks, in addition to kernels, are present. Peduncle growth, both in size and weight, is occurring (see Peduncle Growth section). Lower internodes often increase in dry weight and soluble sugar concentration up to about 2 weeks after anthesis, particularly under conditions of high assimilation; presumably, assimilation exceeds demand and reserves are stored in stem tissue (Asana and Williams, 1965; Rawson and Evans, 1971). Rachis growth seems to be mainly completed by anthesis. Even fewer data are available on rachilla growth, but some rachilla growth must occur after anthesis to allow space for kernels that are growing. Most chaff growth (glumes, paleas, and lemmas) is completed shortly after anthesis (Asana and Williams, 1965), although once again few data are available. One sink often ignored during grain filling is the roots. Belford *et al.* (1987) report that seminal roots grow until anthesis. It is unclear if new root branches develop after anthesis or if significant root extension occurs, but clearly roots continue to function until shortly before maturity (e.g., Anderson *et al.*, 1991; Austin *et al.*, 1977a; Grieve *et al.*, 1981; Heitholt *et al.*, 1990; Smith *et al.*, 1983; Spiertz and de Vos, 1983).

The primary photosynthate source during grain filling is leaves. Almost all assimilates translocated from flag leaves move upward to the grain (Carr and Wardlaw, 1965; Lupton, 1966; Patrick, 1972), whereas the penultimate and third leaves translocate both upward and downward (Lupton, 1966). As a general rule, assimilate is translocated preferentially to the closest sink (Rawson and Hofstra, 1969). The flag leaf is the main leaf source of assimilates to the spike (Patrick, 1972). Maximum LAI is typically reached shortly before anthesis, and often each culm has two to five green leaves present at anthesis. Whether maximum LAI is correlated with maximum photosynthetic activity, however, is debatable, but normally a decline in flag leaf net CO₂ assimilation is observed after anthesis (Araus *et al.*, 1987; Carr and Wardlaw, 1965; Hunt and van der Poorteen, 1984). Given that net carbon exchange rate (CER) decreases with leaf age, canopy net CER should decline even if LAI remains constant as maturity is approached. Leaf sheaths are another source of photosynthate during grain filling, although they have much lower photosynthetic rates than do leaf lamina (Araus *et al.*, 1987; Stoy, 1965).

Spike components can be a potentially important photosynthate source. The assimilate contribution by spike components is variable, with some estimates that the contribution just offsets spike respiration and other estimates that up to 35% of the spike dry weight is derived from spike assimilation (Carr and Wardlaw, 1965; Evans and Rawson, 1970). Carbon exchange rates for spikes were about

90% of flag leaf CER, and awns could contribute from 40 to 80% of the total spike CER (Blum, 1985).

Stem tissue also has some photosynthetic capacity, especially the uppermost portion of the peduncle that is not covered by the flag leaf sheath. Photosynthetic rates of peduncles are lower than those of leaf lamina (Stoy, 1965). Stem tissue can also act as a source in the sense of storing carbohydrates that can be used later in grain filling if needed. Stem nonstructural carbohydrate reserves at anthesis seem adequate to supply much of the grain-filling needs (Evans and Wardlaw, 1976; Gallagher *et al.*, 1975, 1976; Stoy, 1965), although rarely do reserves contribute more than about 30–40% to final grain yield (Aggarwal and Sinha, 1984; Bidinger *et al.*, 1977; Gent, 1994; Palta *et al.*, 1994; Rawson and Evans, 1971; Richards and Townley-Smith, 1987). If translocation from stem reserves does not increase under water stress conditions (Rawson *et al.*, 1977), then the ability of the plant to access the reserves may be limited. Mobilization of stem carbohydrate reserves seems variable among cultivars (Austin *et al.*, 1977b; Blum *et al.*, 1983). Stem reserves have been postulated to serve primarily as a backup for when photoassimilation after anthesis is strongly inhibited and photorespiration rates are increased (Aggarwal and Sinha, 1984; Bidinger *et al.*, 1977; Rawson *et al.*, 1977), which is common under dryland conditions in areas such as the Great Plains.

About 63% of the net assimilation from anthesis to maturity went to the spike (Bremner, 1972). Leaf and stem photosynthetic rates remain high well into grain filling (Araus *et al.*, 1987), and assimilation rates are in part controlled by feedback from the sinks (Blum *et al.*, 1988).

V. CONCLUSION

The dynamic complexity and interaction of development, phenology, and growth challenges our ability to understand shoot apex ontogeny and growth. Simulation modeling potentially provides a puissant and heuristic tool for helping to summarize and integrate much of the research outlined here. However, of the more than 73 models that predict wheat yield (McMaster, 1993), very few (McMaster *et al.*, 1992a,b; Rickman *et al.*, 1996; Weir *et al.*, 1984; Wilhelm *et al.*, 1993) simulate near the level of shoot apex functioning. It is hoped that this review will provide the outline for building the foundation of new wheat simulation models, and that necessary references are discussed. However, much work is still necessary to understand the general developmental pattern (Fig. 3) and how abiotic and biotic factors influence the developmental pattern, both qualitatively and quantitatively. Perhaps the best legacy to be hoped from this effort is a clearer understanding of the gaps in our knowledge.

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