Chapter 2
Development of the Wheat Plant

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SUMMARY

(1) Wheat development is important in creating structures such as leaves and roots needed to capture resources, and also to create the structures ultimately needed to produce viable seed or the desired quality for grain.

(2) Wheat canopy development can be considered at many scales of the plant but often is first viewed at the highest scale of the whole-plant canopy. The canopy can also be considered as the result of the appearance, growth, and abortion or senescence of shoots or tillers. At the lowest scale, each shoot consists of a basic phytomer unit.

(3) A phytomer unit is normally considered to be the leaf, the node plus internode above the node, and an axillary bud. The axillary bud gives rise to new shoots. The root nodal bud should also be considered part of the vegetative phytomer unit. A shoot therefore can be viewed as the appearance, growth, and abortion or senescence of phytomers, or components of the phytomers, that leads to dynamically changing canopies over the growing season and among years.

(4) Regardless of the scale considered, morphological naming schemes have been developed to uniquely identify all parts of the plant, and phenology growth staging scales describe the progress of the tiller or canopy through the life cycle.

(5) Wheat development is orderly and predictable. Genetics provides the orderliness, and environmental factors, mainly temperature, are used to predict development. Thermal time is used as an estimate of the biological clock the wheat plant uses to mark time. Thermal time can be calculated many different ways, but most fundamentally an average temperature is estimated over a time interval (often daily) and used in a temperature-response function to determine the effectiveness of temperature on development rate.

(6) The external phenological progression through the life cycle has also been coordinated with developmental events occurring at the shoot apex, resulting in the complete developmental sequence of the tiller or canopy.

(7) Simulation models of wheat have increasingly incorporated these developmental concepts to varying degrees.

(8) Much of the work describing wheat development is quite empirical, but molecular biology is contributing newfound understanding to underlying genes and mechanisms controlling developmental events. Genetic pathways controlling flowering and plant stature are notable achievements in new understanding.

INTRODUCTION

Development and growth are related, but distinct, processes. As with many terms, precise definitions that satisfy all can be difficult. Therefore, for the purpose of this chapter, growth is defined as the permanent increase in volume, and development is the initiation and

differentiation of organs and the progression of stages through which cells, organs, and plants pass during their life cycle. Often, but not always, growth and development occur simultaneously.

J.W. von Goethe recognized the orderly development of plants in the late 18th century. Since that time, extensive research has quantified the orderly and predictable nature of how the wheat plant proceeds from germination through its life cycle to maturity. This orderliness is observed at all scales of the wheat plant, from the whole canopy to the whole shoot, as well as within the shoot. Genes determine the orderly sequence of wheat development, and the rate and timing of development respond to environmental conditions.

Development serves two purposes. First, it creates the structures such as leaves, roots, and stems needed to capture resources (e.g., light, water, nutrients) that are then used to produce a viable seed. Second, development produces the inflorescence structures needed to produce a viable ovule that can be pollinated at anthesis. Therefore, development is essential in producing the yield potential and the ultimate realization of that potential in final yield.

This chapter discusses the development of the wheat plant. Given the vast research on wheat development and extensive breadth of aspects that can be covered, the goal is to capture and challenge current thinking about wheat development as it fits into the overall purposes of this book. This chapter examines, first, different scales of wheat development, and second, how a shoot develops since the canopy is merely a collection of shoots. The underlying building block of a shoot is the phytomer, and this is discussed to better understand shoot or canopy development. Environmental impacts on development are considered, particularly the critical role of temperature. This chapter presents an overview of simulating wheat development and concludes with new information emerging from molecular biology that provides better mechanistic understanding of wheat development.

SCALES OF PLANT DEVELOPMENT

A cursory walk through a wheat field readily exposes the dynamic nature of wheat development, with many different scales to consider (Masle-Meynard and Sebillotte 1981). Variation in seedling emergence or among wheat spikes that are spatially distributed and differing in size and greenness reflect variation in the canopy. This variation likely will be greater in a larger field with varying soils and topography than within small areas within a field. Further variation might be introduced by variation in genes within a plant community (e.g., single cultivar or multiple cultivars) which control development, though breeders attempt to minimize this variation within a given cultivar. A higher level of resolution is represented by the shoots that comprise the canopy. Examination of individual shoots reveals other differences, such as height, leaf number and size, and stage of development, and this is the result of the basic building block of a shoot, the phytomer. Therefore, at least three scales of plant development can be important: the canopy, the shoot, and the phytomer. Selection of the appropriate scale is dependent on the research or production problem and level of understanding desired.

Canopies

A wheat field is the collection of plants that form the canopy. Plants emerge and grow at different rates, and some die prematurely. Differential patterns of seedling emergence cause some of the variation in development observed in the field. The pattern of seedling emergence varies greatly depending on many nongenetic factors that affect germination and seedling emergence such as planting depth and rate, and soil moisture, temperature, and strength. These factors are highly dependent on the climate, soils, and management practice; spatial variation even at the microscale of less than one meter can cause variation in seedling emergence. Genetic factors such as strength of seed dormancy will influence the pattern of seedling emergence, but even expression of this

trait is not completely independent of environmental influences.

The importance is that the pattern of seedling emergence is reflected in variation in the development observed within a field throughout the growing season. For instance, seedlings that emerge earliest normally are bigger, reach developmental stages earlier, and are higher yielding than those seedlings that emerge later (Gan and Stobbe 1995). Interestingly, although seedlings that emerge later may reach developmental stages later, their development rate often is faster. However, the increased development rate is insufficient to offset their delayed emergence; thus they may still reach maturity slightly later (Nuttonson 1948; Angus et al., 1981; O'Leary et al., 1985) or, if simultaneously, then at the cost of reduced growth.

Shoots or tillers

The canopy is a collection of shoots or tillers which appear, grow, abort, and ultimately senesce, albeit at variable rates among individuals within the canopy. The cumulative number of shoots that appear is dependent on many factors, including the density of plants, the genotype, the environment, and management (Darwinkel 1978; Masle-Meynard and Sebillote 1981; Fraser et al., 1982; Masle 1985). Seedling emergence is important not only in determining the number of plants, but also in determining the number of shoots that a plant produces that will likely survive to produce a spike. This is because a specific axillary bud that produces a tiller has a window of time during which it can appear (Klepper et al., 1982), and once this window passes, that axillary bud will not further differentiate and grow. In most instances, tillers that appear the earliest and from axillary buds on the main stem will be the last ones to abort. This has implications for final yield prediction, as these tillers and the main shoot (i.e., the first shoot to emerge from the seed) are the primary yield-producing shoots (Power and Alessi 1978; McMaster et al., 1994).

Some propose that because the main shoot is usually the most productive, management should focus on producing stands of uniculm plants (i.e., only main shoots). Producing tillers, particularly those that abort before physiological maturity, merely "waste" resources. This approach seems most viable for high-production environments that are less variable in precipitation and extreme events. In highly variable environments, such as many semiarid wheat production regions, tillering can partially adjust for winter kill and other causes of plant loss, and it can provide an adjustment for planting rates normally used that are less than optimal for favorable years (McMaster et al., 2002). Further, when planting at high densities and reducing tiller spikes, main-stem spikes usually will be less productive, so little gain is obtained by the uniculm approach.

Just as later emerging plants usually require less thermal time (i.e., fewer growing degree-days) to reach a given developmental stage, the same has been observed for shoots that appear later, as well as the variation among the main stem and different tillers in reaching a developmental stage being reduced as the plant approaches physiological maturity (Hay and Kirby 1991). This increasing synchrony among shoots results in less canopy variation over time.

Despite differences in developmental stage among shoots on the plant, the pattern of development is the same for each shoot. Further, the response to environmental factors is similar among shoots, although specific responses of individual shoots will vary because they are in different environments within the canopy and the vascular connections and root systems of each shoot will be different. This will be discussed in greater detail later in the chapter.

Phytomers

The shoot is composed of subunits, or building blocks, called phytomers (Gray 1879; Bateson 1894). The phytomer has generally been defined as the leaf, node, internode above the node, and the axillary bud (Wilhelm and McMaster 1995). Each phytomer component can appear, change over time, and/or abort or senesce. In wheat,

prior to the beginning of stem elongation, each phytomer has a minimal internode. The node is the region where the leaf attaches to the shoot and the vascular tissue connects the shoot and leaf; the nodes are closely stacked just below the shoot apex located in the crown of the plant. Once the signal to begin internode elongation occurs, the intercalary meristem of the most recently formed node at the apical region of the node begins cell division and expansion that extends the shoot apex above the crown and ultimately to the top of the canopy. Similarly, the leaf appears, grows, and ultimately senesces. The axillary bud can produce either another shoot, as in wheat, or an inflorescence structure (e.g., either a shoot or the ear of maize, *Zea mays* L.).

For plants such as wheat that can produce nodal roots, the phytomer concept should be expanded to include this component (Forster et al., 2007). Given this definition, generally the phytomer has been viewed as a vegetative building block, yet it is clear that the basic unit is repeated throughout the grass inflorescence (Forster et al., 2007).

The phytomer concept has proven to be a useful botanical abstraction for providing a foundation to understand plant development and architecture. It is the appearance, growth, and senescence of these phytomers that determine the characteristics of individual shoots. This dynamic interplay of phytomers can be considered analogous to a composition of music called a canon (a familiar simple form being a round), where individual phytomers repeat a part against and with other phytomers as do the melodies of a canon (Hargreaves and McMaster 2008). Similarly, the integration of these phytomers within a plant has been outlined in a generic pattern by Rickman and Klepper (1995) for a variety of grasses. This is an excellent demonstration of the consistent and orderly development of the grass shoot apex.

MORPHOLOGICAL NAMING SCHEMES

Naming schemes which uniquely identify each part of the plant can have many advantages. Certainly they aid in communicating precisely what part of the plant is being measured. Naming schemes also can provide insight into how the plant perceives its environment and the efficacy of management practices. Although various nomenclatures have been proposed and modified, most are quite similar.

Leaves

A simple leaf-naming scheme has been proposed by Jewiss (1972) and Klepper et al. (1982, 1983a), in which true leaves (not including the coleoptilar leaves) are numbered acropetally for each culm. The first leaf is designated L1, with successive leaves L2, L3, up to the last leaf formed on the shoot (i.e., the flag leaf). A numerical leaf staging system was proposed by Haun (1973):

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

in which 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 sheath of the penultimate leaf.

One increasingly important application of knowing leaf number in crop management is that many pesticides are to be applied at certain leaf stages. For instance, the herbicide imazamox is to be applied at the fourth-leaf stage for control of many grass weeds when growing the cultivar Above.

Tillers

The system first proposed by Jewiss (1972) for naming tillers has been modified and extended (Masle-Meynard and Sebillotte 1981; Fraser et al., 1982; Kirby et al., 1985a; Masle 1985). The modified system proposed by Klepper et al. (1982, 1983a) is increasingly being adopted. In this system, the leaf axil and parent culm are used to name the tiller. The first culm to emerge from the seed is the main stem (MS), with subsequent new culms being tillers that can be considered primary, secondary, tertiary, and so on, based on the parent culm. Tillers appearing from axillary buds in the

axils of leaves on the MS are considered primary tillers, those from axils of leaves on primary tillers are secondary tillers, and so on. All tillers are designated with a "T" and then numbers. For a primary tiller, the number is a single digit that refers to the leaf number with which the axillary bud is associated. For example, T1 is the tiller emerging from the first leaf (L1) on the MS. Secondary tillers are given a two-digit designation, with the first digit referring to the primary tiller number and the second digit referring to the leaf number. For example, T21 is the tiller emerging from the first leaf (L1) on the primary tiller T2. This system continues for tertiary tillers with a three-digit designation, and so on. The somewhat anomalous coleoptile tiller, which emerges from the axil of the coleoptile leaf, is designated as either T0 (Klepper et al., 1982, 1983a) or TC (Kirby and Eisenberg 1966; Kirby and Appleyard 1984).

Knowledge of the presence or absence of specific tillers has been used to provide information on how the wheat plant perceives its environment. For instance, the proportion of T0 tillers present can indicate the seedbed conditions for seedling emergence. Also, in returning to the window of time that a tiller can appear, the absence of a given tiller indicates conditions were sufficiently stressful to prevent the development and growth of the axillary bud.

Inflorescence parts

The leaf and tiller morphological naming schemes have been extended to the wheat inflorescence. Klepper et al. (1983b) devised a numerical index for the developmental stages of the inflorescence, which extended phenological growth staging scales discussed later in this chapter. However, the morphological naming scheme was not completely developed. Wilhelm and McMaster (1996) proposed a spikelet-naming scheme similar to the leaf-naming scheme: the first spikelet at the base of the spike is designated S1, with subsequent spikelets numbered acropetally until the terminal spikelet. Each floret is also numbered acropetally from the base of the spikelet (e.g., F1, F2, etc.). If referring to the caryopsis, then "C" is used rather than "F" for floret. Each part of the inflorescence can be identified by combining the spikelet and floret/caryopsis designations. For instance, S1F1 refers to the basal floret on the first spikelet of the inflorescence. If the shoot-naming scheme is added, the specific inflorescence on the plant can be identified (e.g., T1S1F1). As with tillers, missing florets or spikelets, or very small caryopsis, indicates a stressful condition leading to abortion or reduced growth of these organs.

Roots

The wheat root system consists of seminal and nodal roots. Seminal roots (usually five to six roots from one seed) are those originating from primordia found in the seed, and nodal roots are those produced from primordia developed after germination (Klepper et al., 1984). The naming system created by Klepper et al. (1984) applies to both seminal and nodal roots. At each node of the shoot, two roots can appear at opposite sides of the node (X and Y zones); two other roots can appear at opposite sides of the node (A and B zones), but rotated 90° from the X and Y zones. Naming schemes for shoots can be applied for nodal roots, with seminal roots originating from the MS. In this system, the timing of root appearance is integrated with leaf appearance (Rickman et al., 1995). The timing, appearance, and growth of tillers and roots as a function of nitrogen fertilizer was examined and found to be strongly impacted by N fertility (Belford et al., 1987).

SHOOT DEVELOPMENT

Morphological naming schemes allow for nondestructive identification of plant parts and provide a context for understanding the developmental processes leading to the appearance, growth, and abortion or senescence of the plant parts. The developmental processes leading to the plant parts are a result of the developmental sequence of the shoot apex and the external developmental stages of the entire shoot (i.e., phenology). Most developmental events occurring at the shoot apex cannot be observed without destructive sam-

pling and often magnification. The external developmental stages have traditionally focused on developmental events that can be observed fairly readily without magnification or destructive sampling.

Phenology

Human cultures have long recognized that plants go through fairly consistent stages of development each year. Common terminology has often referred to these stages as growth stages, but developmental stages is the more appealing term as often little "growth" is involved in the developmental event (e.g., anthesis and physiological maturity). Many so-called growth staging scales have been developed to describe wheat phenology, with many similarities between them (e.g., Frank et al., 1997). Discussions and comparisons among some scales are provided by Bauer et al. (1983), Landes and Porter (1989), and Harrell et al. (1993, 1998).

Of the many growth staging scales, four currently have the greatest usage: Feekes (Large 1954), Zadoks et al. (1974), Haun (1973), and the BBCH Scale (Lancaster et al., 1991). All scales consider some basic developmental events such as germination and emergence, leaf production, tillering, internode elongation, flowering or anthesis, stages of grain ripening, and physiological maturity (Fig. 2.1), with particular scales emphasizing different processes.

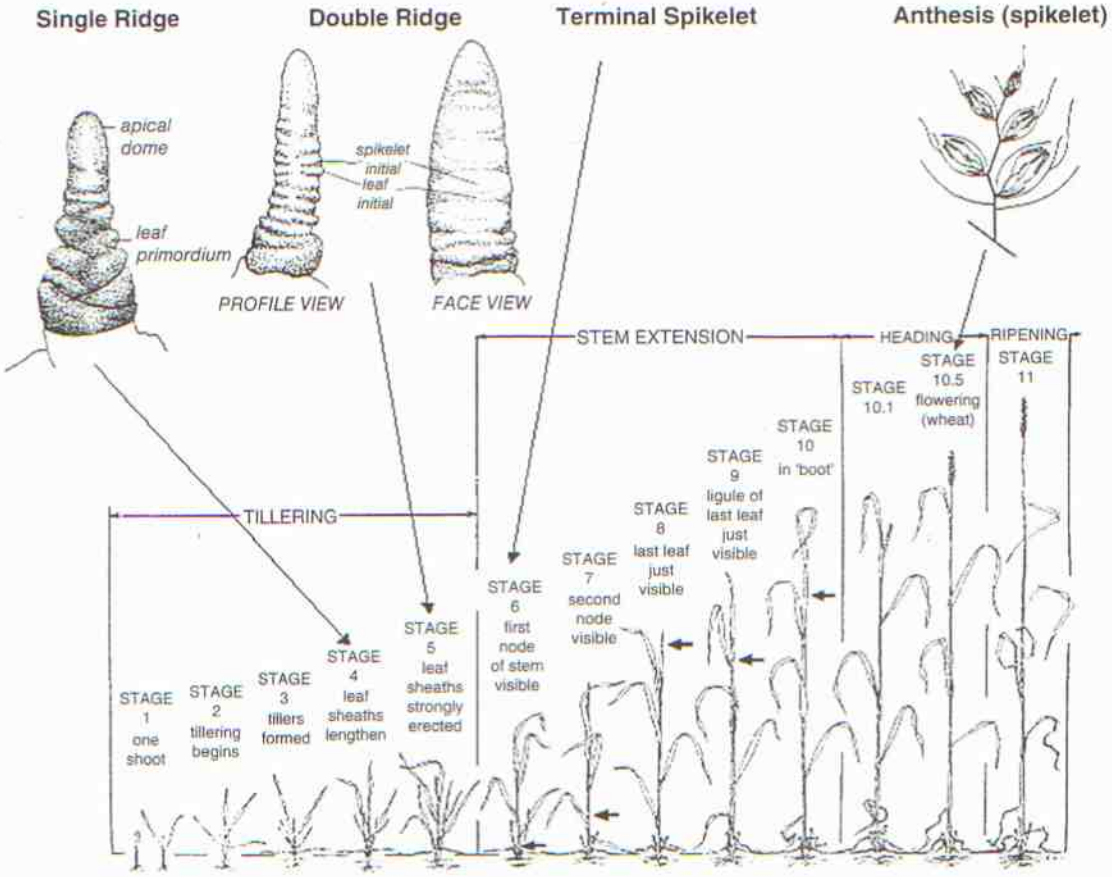

Fig. 2.1 The Feekes growth stage scale (Large 1954) correlated with the approximate timing of certain shoot apex developmental stages. See Table 2.1 for descriptions of developmental stages. (Adapted from McMaster 2005.)

All cultivars and each shoot go through the same developmental event (again, this is the orderliness of plant development), but cultivars and shoots vary on the timing (beginning and ending of the developmental event) and duration. This is a result of both differences in genotype and the cultivars' responses to environmental conditions. The period of grain filling illustrates this well. Cultivar trials clearly demonstrate that within the same environment cultivars vary in the time of internode elongation, anthesis, and physiological maturity, and that this also affects the duration of grain filling. Synchrony among shoots in reaching a developmental stage increases as physiological maturity is approached (Hay and Kirby 1991).

Clear definitions of many developmental stages are not always reported. Descriptions for the Feekes (Large 1954) and Zadoks (Zadoks et al., 1974) scales are provided in Table 2.1. For instance, the start of internode elongation and the developmental stage of jointing are two stages with some ambiguity, particularly for determination in the field. Both scales only discuss stem elongation in terms of when nodes are above the soil surface; therefore the beginning of internode elongation is earlier than this, as often the first node is formed below the soil surface. Jointing in the Feekes scale is defined as when the first node is observed to be one inch (2.54 cm) above the soil surface, although many practitioners merely record when the node is first observed at any distance above the soil surface. The time in which internode elongation begins prior to jointing is difficult to discern in the field without destructive sampling; thus internode elongation is sometimes erroneously assumed to begin at jointing. The concept of first-hollow-stem stage was created to call attention to the developmental difference between initiation of internode elongation and jointing in wheat production systems with grazing cattle (*Bos taurus* L.). Producers depend on staging to know the proper time to remove cattle from wheat pasture just before jointing so that further development and extension of the shoot apex is not impaired (Redmon et al., 1996).

Booting is defined as the stage when the spike can be felt within the whorl of leaf sheaths but is not visible. Given the ambiguity of measuring this stage relative to when booting actually begins and that it is a continuum until heading, a useful definition is to assume booting begins when the flag leaf has formed its ligule and continues until heading. Heading is defined as beginning when the first spikelet of the spike (i.e., head or ear) first appears above the ligule of the flag leaf at the top of the canopy. Normally the first spikelet to appear is the terminal spikelet, and heading is completed when the basal spikelet (= S1 in the morphological naming scheme) appears. Generally awns are ignored in observing the beginning of heading, and occasionally the spike emerges "sideways" from the sheath, and many observers consider this heading.

Physiological maturity is somewhat difficult to quantify and to consistently determine among different observers. Unlike maize that has a black layer in the kernel to indicate when maximum dry weight has been reached (the definition of physiological maturity), wheat has no such discernible trait. The Feekes scale defines harvest maturity as when the kernel is difficult to divide along the crease. Similarly, Zadoks et al. (1974) equate 90% ripeness of rice (*Oryza sativa* L.) to when the seed cannot be dented by the fingernail. Neither scale clearly defines physiological maturity. An association of maturity and maximum dry weight has been suggested when all glumes, paleas, and lemmas of the spike have lost all green color; all leaves will have senesced before this time and internodes will have lost all green color (Hanft and Wych 1982). This is a rather obvious time of maximum dry weight, as all sources of new carbohydrates via photosynthesis are gone and reserves should be allocated to grains or exhausted.

The location of the shoot apex changes with developmental stage and has implications for the environment of the shoot apex and certain management practices such as cattle grazing mentioned previously. Until the time that internode elongation begins, the shoot apex is located in the crown of the plant. The crown is normally located

Table 2.1 Description of principal developmental stages in the context of Feekes (Large, 1954) and Zadoks (Zadoks et al. 1974) developmental scales, with suggested measurement characteristics.

Stage	Description	Measurement Characteristics
Germination	Feekes—no stage Zadoks—01 (start of imbibition), 03 (imbibition complete), 05 (radicle emerged from caryopsis), 07 (coleoptile emerged from caryopsis)	Start of imbibition is when the seed begins to swell
Emergence	Feekes—no stage Zadoks—09 (leaf just at coleoptile tip)	Beginning of emergence is when the first true leaf emerges through the coleoptile and tip is visible above the soil surface
Tillering	Feekes—1.0 (main shoot only), 2.0 (beginning of tillering) Zadoks—20 (main shoot only), 21–29 (main shoot and 1 tiller through 9 tillers)	Beginning of tillering is when the first tiller is visible (likely T0 or T1)
Single ridge	Neither scale describes	Begins when the shoot apex shape changes from dome to more elongated, and leaf primordia begin to form a ridge around apex (Fig. 2.1)
Double ridge	Neither scale describes	Begins when the formation of double ridges (bottom ridge = leaf, top ridge = spikelet) around the apex occurs (Fig. 2.1)
Terminal spikelet	Neither scale describes	When the apical spikelet primordium appears and noted by rotation of 90º from plane of previous spikelets
Internode elongation	Neither stage clearly notes the beginning of internode elongation; rather it is assumed to be in stem elongation when node(s) are visible above the soil surface. Feekes—6 (first node of stem visible at base of shoot above soil surface), 7 (second node visible, next to last leaf just visible) Zadoks—31 (first node detectable) through 36 (sixth node detectable)	Beginning of internode elongation is when the first node is visible (but normally will be below the soil surface)
Jointing	Feekes—implicitly assumed to be when the first node is visible above the soil surface (Stage 6) and when plant growth habit changes from prostrate to upright Zadoks—not described	Occurs when first node is visible above the soil surface
Flag leaf	Feekes—8 (last leaf visible but still rolled, ear beginning to swell), 9 (ligule of last leaf just visible), 10 (sheath of last leaf completely grown out, ear swollen but not yet visible) Zadoks—39 (flag leaf ligule/collar just visible), 41 (flag leaf sheath extending, booting)	Cannot know if it is the flag leaf while it is appearing; flag leaf growth is considered complete when the ligule is visible and no new leaf is emerging
Booting	Feekes—see above for 8–10 Zadoks—41 (see above), 43 (boot just visibly swollen), 45 (boot swollen), 47 (flag leaf sheath opening), 49 (first awns visible)	As booting is a continuum, begins when the flag leaf ligule is visible and ends when heading begins
Heading	Feekes—10.1 (first ears just visible), 10.2 (1/4 of heading process completed), 10.3 (half completed), 10.4 (3/4 completed), 10.5 (all ears out of sheath) Zadoks—50 (first spikelet of inflorescence just visible), 53 (1/4 of inflorescence emerged), 55 (half of inflorescence emerged), 57 (3/4 emerged), 58 (inflorescence completely emerged)	Measure based on one inflorescence (main stem best), and heading begins when first spikelet is visible (awns not considered) and ends when the inflorescence has completely emerged from the flag leaf
Anthesis	Feekes—10.5.1 (beginning of flowering, 10.5.2 (flowering complete to top of ear), 10.5.3 (flowering over at base of ear), 10.5.4 (flowering over, kernel watery-ripe) Zadoks—61 (beginning of anthesis), 65 (anthesis halfway), 69 (anthesis complete)	Measure based on one inflorescence (main stem best); ends when first anther (yellow) is visible on inflorescence, and ends when no more anthers appear on the inflorescence
Physiological maturity	Feekes—11.1 (milky ripe), 11.2 (mealy ripe, contents of kernel soft but dry), 11.3 (kernel hard, difficult to divide by thumbnail), 11.4 (ripe for cutting, straw dead) Zadoks—a series of stages from milk development (77–77), dough development (83–87), and ripening and seed dormancy (91–99)	No scale definitively identifies when physiological maturity is reached (defined as maximum dry weight); Hanft and Wych (1982) indicate when all components of the spike (glumes, paleas, lemmas), internode tissue, and leaves have lost all green color

Developmental stage descriptions derived from Bauer et al. (1983) and the original references. Some developmental stages are shown in Fig. 2.1.

at a depth of about 2 to 3 cm below the soil surface. If planting is deeper than this, as is often the case, then the coleoptilar internode will elongate to form the crown at this depth. As the internodes elongate, the shoot apex moves from the soil environment (i.e., crown) into the aerial environment within the canopy. In many wheat production systems, the danger of cold temperatures (i.e., frost) is present at this time and significant damage to the shoot apex spikelet and floret primordia that are forming and differentiating can occur, resulting in yield loss. At heading, the shoot apex or spike emerges above the canopy and the glumes, paleas, lemmas, and awns (if present) are exposed to full sunlight. Primarily the flag leaf and spike photosynthetic tissues contribute new assimilates for grain filling, with the spike contributing up to about 10% of the flag leaf photosynthetic rate (Weyhrich et al., 1995).

Shoot apex

Developmental events occur at many places within the plant; however, the shoot apex is the site of many of the most important developmental events such as leaf, tiller, and inflorescence primordia production. As previously mentioned, these events are not represented in developmental scales (Fig. 2.1). As with phenology, the shoot apex of all cultivars and shoots has the same developmental sequence (Fig. 2.2), but cultivars and shoots vary in the timing and duration of the developmental event. Furthermore, this developmental sequence is generally shared by most grasses, particularly the annual cereal crops such as barley (*Hordeum vulgare* L.) and rice (Rickman and Klepper 1995). Many reviews of wheat shoot apex development are available that provide considerable detail (e.g., Barnard 1955; Bonnett 1966; Kirby and Appleyard 1984; McMaster 1997).

The developmental sequence of the shoot apex begins with the embryo within the seed. Wheat typically has three to four leaf primordia formed in the embryo (Bonnett 1966; Baker and Gallagher 1983a; Hay and Kirby 1991). Once germination of the seed has occurred, further development and growth of the existing leaf primordia occurs, resulting in leaf appearance of L1, L2, and so on. Coinciding with the appearance of the first leaves is the initiation of more leaf primordia. Leaf primordia are initiated up to the stage of double ridge. At double ridge, the leaf primordium forms a ridge around the apex and this primordium will not further differentiate and grow (Fig. 2.1). The ridge above the leaf primordium is the spikelet primordium. Primordia formed prior to double ridge will continue to differentiate and grow resulting in the continuation of leaf appearance until the flag leaf appears, which is about the second leaf to appear after the developmental stage of jointing.

Developing the leaf area index (LAI) of the canopy is a function of the appearance, growth, and senescence of leaves on each shoot comprising the canopy. Leaf size increases on a shoot up to about the 10th leaf, although the flag leaf tends to be slightly smaller than the penultimate leaf (Gallagher 1979; Hay and Wilson 1982; Rawson et al., 1983; Kirby et al., 1985b). Under unstressed conditions, leaves do not begin senescing until about 6.5 phyllochrons (time interval for appearance of successive leaves) after first appearing, and abiotic stresses such as water deficit and low N availability will enhance the senescence rate (McMaster et al., 1991; Wilhelm et al., 1993). Therefore leaves of increasing size accumulate on a shoot, and leaf senescence begins with the smallest and oldest leaves. Generally peak LAI is reached at the time the flag leaf completes growth.

The rate of leaf primordia initiation (plastochron) and appearance (phyllochron) are critical to many subsequent developmental events. For instance, until the leaf primordium has been initiated and begins to grow, the axillary bud that can form a new tiller is not initiated. This is why the beginning of tiller appearance is delayed from leaf appearance in Fig. 2.2. The rate of leaf appearance therefore "controls" the window of time that the tiller can appear. Leaf primordium differentiation and growth also determines the formation of the node, which is the point where vascular tissue enters the leaf.

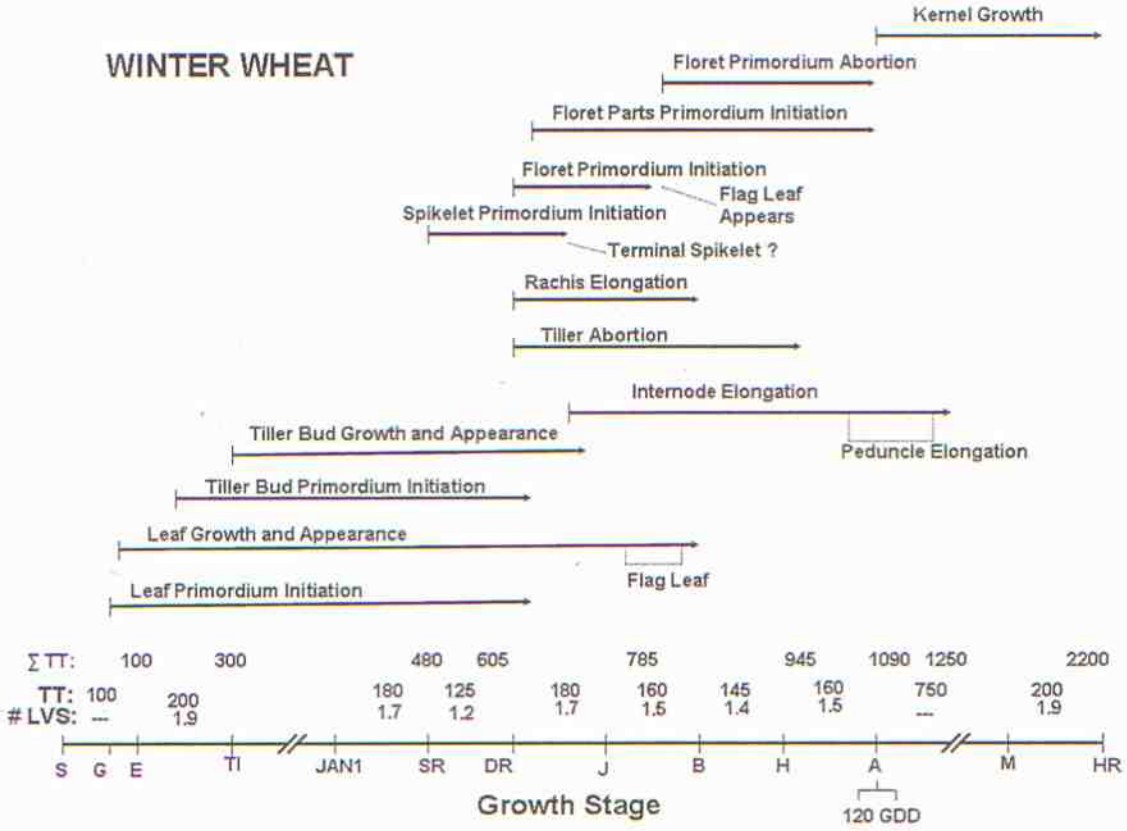

Fig. 2.2 Winter wheat shoot apex developmental sequence correlated with developmental stages (Large 1954) for conditions with no stresses. The timeline is presented as thermal time (TT, in growing degree-days, GDD, using 0°C base and Method 1 of McMaster and Wilhelm 1997) and number of leaves (#LVS). Question marks indicate areas of uncertainty or significant variation among cultivars. See Table 2.1 for descriptions of developmental stages. (Adapted from McMaster et al., 1992b.)

An important transition of the shoot apex is from leaf to spikelet primordium initiation, and this occurs at the double ridge stage. The general rule is the rate of spikelet primordia initiation is about two to three times greater than leaf primordia initiation (Baker and Gallagher 1983a,b; Hay and Kirby 1991). Extensive physiological research has examined the environmental factors influential in determining when this switch occurs. Of these factors, the vernalization requirement and photoperiod sensitivity of the genotype play a critical role in the switch.

Several vernalization genes (*VRN*) have been identified as further discussed in Chapter 3, and their presence or absence determines the vernalization requirement for the genotype. The physiological conceptual model is that cool temperatures are needed to satisfy the vernalization requirement and that vernalization is a process of accumulating days with cool temperatures until a sufficient period of time with cool temperatures has occurred. Winter wheat cultivars with a high vernalization requirement may require 6 weeks or more of cool temperatures to complete their ver-

nalization requirement. Temperatures within the range of about 2–7 °C seem most effective for vernalizing, with decreasing effectiveness below or above this range (McMaster et al., 2008). High temperatures (>30 °C) can also "undo" some of the vernalization (i.e., devernalize) that had previously occurred.

Photoperiod sensitivity varies considerably among genotypes and is the result of which photoperiod (*PPD*) genes are present (also discussed in Chapter 3). The conceptual model is that photoperiod or day length must reach a certain threshold to produce the signal that induces the primordium switch. Cultivars with low photoperiod sensitivity tend to have a low day length requirement so that it is met under most environments. Some uncertainty has existed on how to combine the vernalization and photoperiod responses in developmental models, with the view often held that vernalization requirements must be at least largely met before the photoperiod response can occur (McMaster et al., 2008).

It is difficult to precisely determine the vernalization response and photoperiod sensitivity of a genotype, but efforts to estimate these from loci present in the genotype appear promising (White et al., 2008). Genes for frost tolerance can also complicate the relationship (Prasil et al., 2004). Until recently, the mechanisms and genetic pathways for the developmental switch were not known. Chapter 3 provides an excellent summary of the genetic pathway as currently understood and explains the variation observed among genotypes.

Once spikelet primordium initiation begins at double ridge, spikelet primordia are produced until near the time that internode elongation begins, when the terminal spikelet is initiated (Fig. 2.2). Shortly after a spikelet primordium is initiated, floret primordia are initiated acropetally within the spikelet. Floret primordium differentiation then occurs to produce the structures of the floret. As many as 10 floret primordia may be initiated within a spikelet, and initiation occurs until about when the flag leaf appears. After this time, floret primordium abortion tends to occur basipetally within a spikelet until the time of anthesis. The end result of the overlapping sequence of spikelet and floret primordia initiation is that, in the mature spike, central spikelets begin differentiation first and thus have the longest period for initiating florets and longest time for those florets to fully develop. This is why central spikelets have the most kernels and kernel number declines acropetally and basipetally from central spikelets.

Yield potential has been determined by the time of flowering, as all florets have been produced. Pollination of fully developed florets is critical in determining grain set and final yield. Environmental conditions determine the success of grain set, with temperature and water stress normally the most important factors. In many semiarid wheat production regions, hot and dry conditions can significantly reduce grain set both through loss of pollen viability and early seed abortion.

Wheat is self-pollinated, and pollination follows the pattern of floret primordia initiation within the spike discussed previously. This has implications for final kernel size. Earlier fertilization events allow greater time for seed development and growth, and potentially larger final kernel size. Seed development and growth proceeds through a clear set of steps, and extensive research has been published on that subject [Herzog (1986) and McMaster (1997) cite many references]. Ontogeny of the seed mainly consists of development of the embryo and the endosperm tissue. Embryo development is completed prior to endosperm maturity, with the loss of seed moisture in the endosperm that is necessary for combine harvesting (usually about 120 g kg^{-1} moisture).

Growth of all kernels is characterized by a sigmoidal pattern that is frequently divided into three phases: lag phase, linear phase, and maturation phase (Herzog 1986). The lag phase primarily consists of cell division, the linear phase is driven by maximum cell expansion growth rates, and the maturation phase is mostly the loss of seed moisture. Abiotic and biotic factors strongly influence final kernel size, consummated both by the duration of the kernel growth (primarily the length of the linear phase) and by the rate of growth (the slope of the linear phase). Both

of these growth factors are quite variable among cultivars, but in most instances, the duration of kernel growth is more important than rate of kernel growth in determining final kernel size (Herzog 1986; McMaster 1997). A management consideration in heat-stressed environments is managing when grain filling occurs as a means of avoiding adverse high temperatures.

Figure 2.2 presents a time series of the presence of sources and sinks, and indirectly source and sink activity. Although not shown, root growth is the first main significant plant component early in the life cycle. As leaves and tillers begin to appear, they are initially an equal sink (for growth) as roots. At the time of the initiation of internode elongation, leaf appearance has nearly stopped, and stem tissue is the main sink component for carbohydrates and nutrients. Internode growth is occurring normally at peak canopy LAI and photosynthetic capacity, and this is often a period when carbohydrate reserves are stored in the stem material. When grain filling starts, internode elongation has nearly ceased, and the seeds are the main sink component. Although components overlap somewhat in their primary growth period, a general rule is that only one component is primarily growing at a time.

Integrating phenology, the shoot apex, and phytomers

The orderly development of the wheat plant begins with the developmental events occurring at the shoot apex. By producing the leaf and spikelet primordia on a shoot, the basic building blocks of the phytomers are added to comprise the shoot. The rate of appearance of vegetative phytomers can be determined by rate of leaf primordium initiation (plastochron) or leaf appearance (phyllochron). Similarly, reproductive phytomers in the spike are determined by the rate of spikelet primordium initiation and floret primordium differentiation in the spikelet. While a great number of studies have examined leaf, spikelet, and floret primordium initiation and subsequent growth, equations to accurately predict the rates have not been very successful (McMaster and Wilhelm 1995).

Phytomers (or the subcomponents of a phytomer) appear, grow, and senesce or abort on a shoot (Fig. 2.2). Some phenological stages of the shoot may be defined by the state of a specific phytomer. For instance, the beginning of the boot stage is when the leaf in the last vegetative phytomer (i.e., the flag leaf) has completed growth on the shoot. Often the phenological stage is the result of a collection of phytomers on the shoot. Illustrations of this are: the tillering stage, when axillary buds of different vegetative phytomers differentiate and grow; jointing, which occurs when one or more internodes of vegetative phytomers have elongated so that the first node is elevated above the soil surface; and flowering, which occurs when several reproductive phytomers have produced anthers.

ENVIRONMENTAL FACTORS INFLUENCING SHOOT DEVELOPMENT

The relationship between plant development and the environment was undoubtedly recognized by prehistoric civilizations. While the orderliness of wheat development at various scales outlined above occurs regardless of the environment, abiotic and biotic factors and some management practices change developmental rates and the beginning and ending of the process (and therefore duration). Abiotic factors are used to predict development. The mechanisms of action of management practices and biotic factors are best viewed by how they alter the predictive nature of abiotic factors.

Abiotic factors such as temperature, light, water, fertility, and CO_2 control wheat development, though temperature is viewed as the most important factor (Klepper et al., 1982; Baker and Gallagher 1983a,b; Bauer et al., 1985, 1986; Frank et al., 1987; Porter and Delecolle 1988; Masle et al., 1989; McMaster 2005). Temperature strongly impacts cell cycling time, reaction rates, and progression through the life cycle. Light can strongly influence some developmental events, but the other abiotic factors are considered of

secondary importance and usually affect only certain developmental processes or events (Masle et al., 1989). Further, factors such as water and nutrients often seem to have threshold levels before influencing development. Given the importance of temperature in controlling and predicting wheat development, this section focuses primarily on the role of temperature.

Temperature

Reamur (1735) formalized the relationship between phenology and temperature by creating the concept of heat units, which is more commonly known today as thermal time. Thermal time acknowledges that, for most developmental processes, temperature is a better predictor than calendar time (i.e., days, hours, etc.). Many studies (Friend et al., 1962; Cao and Moss 1989; Jame et al., 1998; Yan and Hunt 1999; Streck et al., 2003; Xue et al., 2004) show a curvilinear response of the developmental process to temperature. Thermal time is an attempt to explain the observed differential response to temperature. Many forms of describing and quantifying thermal time have been developed, yet all forms are empirical in approach as the direct mechanisms of temperature effects are not well known (Wang 1960; Shaykewich 1995; Jamieson et al., 2007).

Estimation of thermal time has two elements: (i) average temperature (T_{avg}) over some time interval and (ii) use of T_{avg} in a temperature-response function to estimate the rate of the developmental process or "passage of time" (i.e., the effectiveness of a specific temperature on development rate). The most accurate calculation of T_{avg} is to use the integral of temperatures over the time interval of interest, but in practice the maximum (T_{max}) and minimum (T_{min}) temperature of the interval are used:

$$T_{avg} = (T_{max} + T_{min})/2 \quad (2.1)$$

This simple estimation of T_{avg} is generally accurate, but errors increase as day length deviates from 12 hours and if sudden changes in temperature occur during the time interval. Selection of the time interval depends on availability of data and the problem, but most frequently a daily time interval is used, with day/night and hourly intervals sometimes used. Somewhat problematic is that equation 2.1 has been interpreted in different ways, resulting in over a 20% difference in the estimation of T_{avg} for a growing season using the same weather data, and it often is unclear how the equation is being interpreted (McMaster and Wilhelm 1997).

Once T_{avg} is determined, a key area of divergence in thermal time approaches is the temperature-response function. The most basic version is to estimate thermal time (TT) linearly above the base temperature (T_{base}) at which the development rate is zero (Fig. 2.3a):

$$TT = T_{avg} - T_{base}, (\mathrm{TT} \geq 0) \quad (2.2)$$

Thermal time in this instance is often expressed as growing degree-days (GDD, °C days), and the value can be either summed or used directly in an algorithm. For example, it may require an average of 105 GDD for a leaf blade to grow completely (Frank and Bauer 1995), or if the final blade length is 105 mm the rate of growth can be 1 mm GDD^{-1}. Normally, predicting when a developmental event begins or ends assumes a summation of thermal time.

The base temperature is important in defining the minimum temperature at which development can occur; T_{base} can be difficult to directly measure, and it likely changes both among cultivars and possibly with progression through the life cycle (Angus et al., 1981; Weir et al., 1984; McMaster and Smika 1988; Slafer and Rawson 1995a,b; Madakadze et al., 2003). Yet often this does not introduce significant error for predicting development in the field, as little development occurs near T_{base}, inaccuracies in calculating T_{avg} mask slight differences in setting T_{base}, and little difference in predictive accuracy is noted by using a range of temperatures for T_{base} (McMaster and Smika 1988). Often T_{base} is set to 0 °C (Gallagher 1979; Baker and Gallagher 1983a,b; Slafer and Rawson 1994; McMaster et al., 2008).

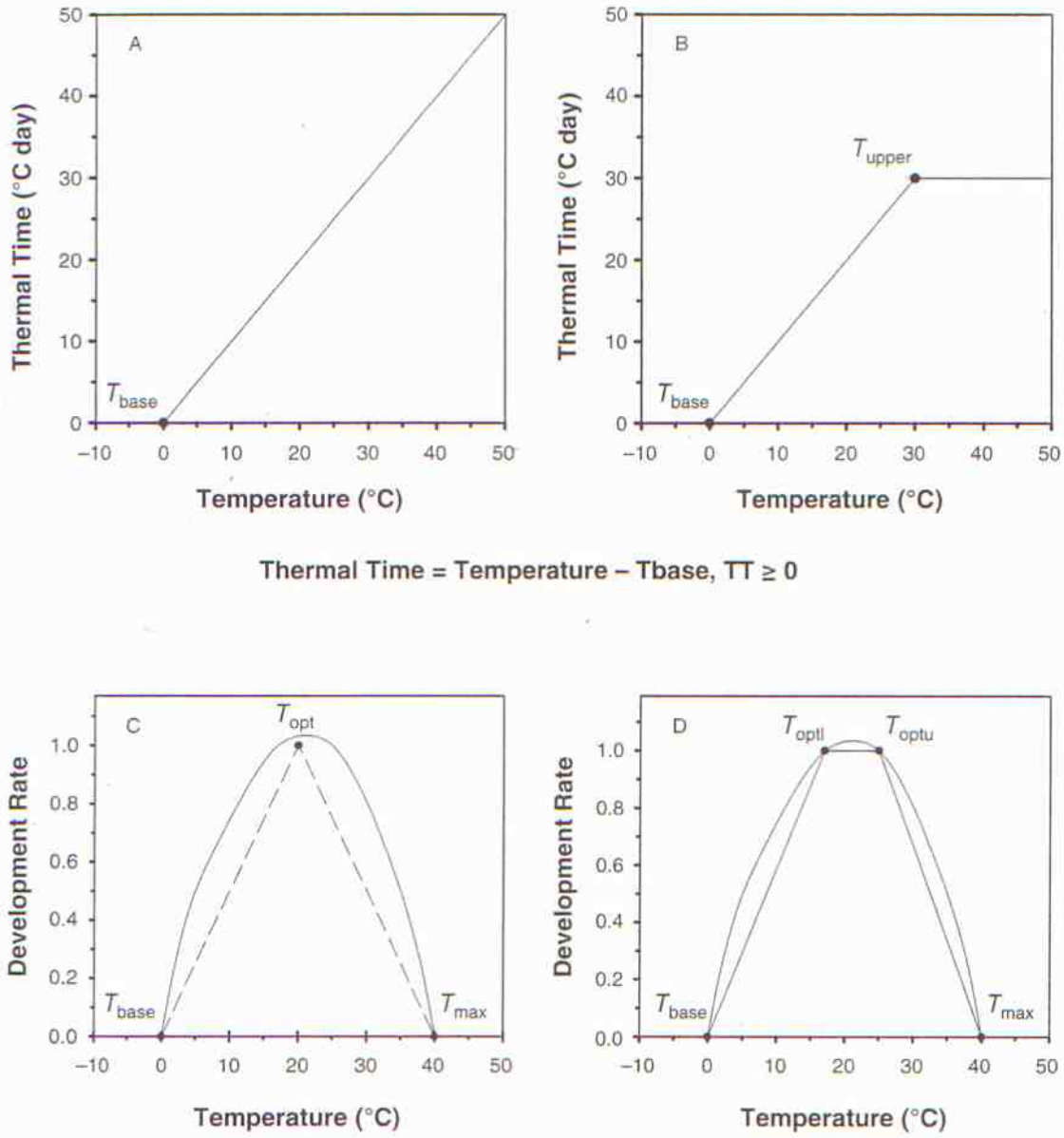

Fig. 2.3 Development rate as a function of temperature. Examples of different approaches for estimating thermal time are shown in each graph. Curvilinear temperature response function shown in parts c and d are based on Friend et al. (1962), Cao and Moss (1989), and Jame et al. (1998). T_{base} is the base temperature (i.e., development rate is zero), T_{opt} is the optimum temperature (i.e., development rate is at the maximum), T_{optl} and T_{optu} are the lower and upper temperatures for the optimum temperature range, and T_{max} is the maximum temperature (i.e., development rate is zero).

Equation 2.2 uses only one cardinal temperature (T_{base}) in calculating thermal time, and as temperature increases so does the development rate. Incorporating a second cardinal temperature for an upper temperature threshold into equation 2.2 recognizes that development rate does not increase indefinitely with temperature. Upper threshold temperatures, if used, are generally set to at least 30 °C when used in equation 2.2 and limit accumulated thermal time to the upper threshold (Fig. 2.3b). Most wheat production systems do not often exceed average daily temperatures greater than 30 °C, and therefore, errors in setting this upper threshold seem relatively minor for field predictions (McMaster et al., 2008).

If another cardinal temperature, related to the optimum temperature (T_{opt}) for development rate, is added along with changing the definition of the upper temperature threshold to be the maximum temperature that development rate is greater than zero (T_{max}), then a better representation of the observed normal temperature-response curve is improved. A two-segmented linear model can be used with thermal time increasing linearly from T_{base} to T_{opt}, then linearly decreasing from T_{opt} to T_{max} (Fig. 2.3c). Dividing T_{opt} into a lower (T_{optl}) and upper (T_{optu}) temperature optimum, between which development rate is maximum, results in a three-segmented linear model that closely approximates the observed temperature response curve (Fig. 2.3d). The final adjustment is to use a curvilinear model such as those proposed by Yan and Hunt (1999) and Streck et al. (2003). If the curvilinear models are parameterized correctly, they should mimic the observed temperature-response function shown in Fig. 2.3c,d.

Largely because air temperature is more readily measured and available, it is used in calculating T_{avg}. The assumption is that the relationship between air temperature and shoot apex temperature (where many developmental events occur) is closely associated. Theory would suggest using either soil temperature at the depth of the shoot apex (approximately 2–3 cm) when the shoot apex is located in the soil or plant canopy temperature when the apex is located in the plant canopy (Peacock 1975). Experimental support for this theory is related to a long history of root–shoot temperature experiments (Hay and Wilson 1982; Jamieson et al., 1995; Stone et al., 1999; Vinocur and Ritchie 2001). However, the possible theoretical gain of using soil and plant canopy temperature was not always realized in the field for wheat (McMaster and Wilhelm 1998; McMaster et al., 2003). This was explained by (i) the shoot apex and other intercalary meristems such as for leaf growth are located over a vertical space where temperatures vary considerably (Skinner and Nelson 1995), (ii) the whole plant senses temperature and that influences signal and resource movement throughout the plant, and (iii) the relationship between air temperature and shoot apex temperature is quite stable in many environments.

All developmental processes show the curvilinear response to temperature shown in Fig. 2.3c,d. However, the duration of grain filling, a critical component of determining final yield, merits special mention here. As temperature increases, both grain filling rates and the accumulation of thermal time are increased. The net effect of these two responses is that kernel weight usually is less under higher temperatures than cooler temperatures because the duration of grain filling is decreased more than the rate of growth is increased (Marcellos and Single 1971; Sofield et al., 1974; Wiegand and Cuellar 1981; Bhullar and Jenner 1983; Herzog 1986; Wardlaw et al., 1989).

Nontemperature environmental factors

Environmental factors in addition to temperature can influence wheat growth and development, but it is difficult to summarize the diversity of responses, or nonresponses, to various environmental factors. Cultivars can vary in their responses to similar treatments, and of course, the ever-present genotype × environment interaction further complicates understanding the responses. Many experiments, particularly those in the field, have not carefully measured the level of the environmental factor, the levels change during the course of the experiment, and an insufficient number of treatments are applied to fully understand and quantify the response surface. This has

resulted in a qualitative understanding of response; however, quantitative characterization of the response is often lacking and identification of threshold levels for a factor is unknown.

Regardless of these difficulties, one general rule is that growth of an organ is reduced and abortion or senescence rates are increased when the environmental factor is limiting. For instance, leaf, internode, and kernel growth is reduced and leaf senescence and tiller, spikelet, and floret abortion is increased when water, nutrients, CO_2, or light is limiting or under high salinity conditions (Gifford 1977; Whingwiri and Kemp 1980; McMaster et al., 1987; Maas and Grieve 1990; Jedel and Hunt 1990; Maas et al., 1994).

Although temperature and photoperiod are the most important factors controlling wheat phenology, phenological responses to water availability have been reported (Angus and Moncur 1977; Bauer et al., 1985; Baker et al., 1986; Frank et al., 1987; Davidson and Chevalier 1987, 1992). McMaster and Wilhelm (2003) observed that later developmental stages, particularly anthesis and physiological maturity, were most sensitive to water deficits and required less thermal time to reach the developmental stage under water deficits than well-watered conditions. Most notably, the grain filling duration was significantly reduced by water deficits, as commonly observed in many experiments and for most crops (McMaster et al., 2009). In general, water deficits must be quite substantial before phenological responses are noted. Physiological and genetic mechanisms controlling these phenological responses are not well understood, but the likely indirect effect of water deficits increasing canopy temperature, and therefore thermal time accumulation, might partly explain the general response of reaching a developmental stage earlier under water deficits (McMaster et al., 2009).

Occasional responses of some developmental stages to nutrients have been reported (Frank and Bauer 1984). At low levels of N, developmental stages such as double ridge, terminal spikelet, and anthesis were delayed (Whingwiri and Stern 1982; Longnecker et al., 1993). Nitrogen limitation seems to have the greatest effect on decreasing the duration of grain filling, presumably by increasing leaf senescence. Other factors have a less reported or consistent effect on phenology than nutrients. For instance, if ambient CO_2 levels were doubled (700 ppm), the time required to reach floral induction and anthesis was slightly shortened (Marc and Gifford 1984), and the spikelet, floret, and grain filling development phases were reduced by elevated CO_2 (550 ppm, Li et al., 1997, 2000).

Leaf, spikelet, and floret primordia initiation appears to be minimally reduced by factors other than temperature and light, although leaf appearance and final spikelet and floret number are often reduced by factors other than temperature and light (Whingwiri and Stern 1982; Longnecker et al., 1993; Li et al., 1997). Three possible explanations that are not mutually exclusive could account for the variable responses noted. One explanation has been mentioned before: until a threshold level is reached, little response to an abiotic factor is observed. An example of this would be the response of reduced spikelet primordium initiation and delayed developmental stages observed only at low levels of N (Longnecker et al., 1993). Another explanation is that the duration of the phase is shortened by the abiotic factor that affects the final number of primordia initiated. An illustration of this would be Frank et al. (1987) showing that water stress mainly affected spikelet primordium initiation by decreasing the initiation phase. The third explanation for the reduced response of many developmental processes to environmental factors is that primordium initiation mainly responds to hormonal controls and then is driven by cell cycling time, which is primarily a temperature-response process that requires little resources in terms of water and nutrients. If these resources are limiting to the extent that cell division is impacted, then in annual plants such as wheat, the shoot or shoot apex is in danger of death. However, the differentiation and growth of these primordia (e.g., leaves, tillers) are strongly influenced by many environmental factors

(Frank and Bauer 1982, 1984; Bauer et al., 1986; Maas and Grieve 1990; Cutforth et al., 1992), and this might be hypothesized to be the result of lack of resources required for growth of the organ.

As an illustration of this, leaf primordia initiation showed little response to elevated CO_2 (Li et al., 1997), yet a slight positive relationship between CO_2 and the rate of leaf appearance seems to exist (McMaster et al., 1999). Similarly, differentiation and growth of the axillary bud, resulting in the appearance of a new tiller, is strongly regulated by water, nutrients, and carbohydrate availability, as well as light intensity and quality, although the relationship is sometimes stronger for tillers than the main stem (Fraser et al., 1982; Longnecker et al., 1993; Maas et al., 1994). Further, younger tillers or secondary and tertiary tillers often respond more to resource limitations. One hypothesis is that these tillers are most dependent on the whole plant for resources that every shoot is competing for and are farthest removed from access to the resource in terms of vascular connections (water, nutrients, and so on) or location within the canopy (i.e., light intensity and quality).

DIGITAL TECHNOLOGIES FOR WHEAT DEVELOPMENT

Probably more digital technologies are available for modeling wheat growth and development than for any other crop. Digital technologies include simulation and regression models, decision support systems (DSS), web sites, and specific computer programs. This section will briefly focus on simulation models as related to wheat development.

Many models simulate wheat production and yield (McMaster 1993), and at the risk of omitting many deserving models, several that have been of historical significance or played an influential role in wheat modeling include AFRCWHEAT1/2 (Porter 1984, 1993; Weir et al., 1984), APSIM (Asseng et al., 1998), DSSAT/CERES-Wheat/CropSim (Ritchie and Otter 1985; Ritchie 1991; Hunt and Pararajasingham 1995; Jones et al., 2003; Hoogenboom et al., 2004), Sirius (Jamieson et al., 1995, 1998), SUCROS (van Laar et al., 1992), SWHEAT (van Keulen and Seligman 1987), and WINTER WHEAT (Baker et al., 1985). A diversity of approaches exists in how growth and development are simulated in these wheat process-based models. However, for most simulation models, the earliest approaches that still remain popular today use the energy- or carbon-driven approach, in which sunlight energy is captured by the plant, converted to biomass, and then partitioned within the plant. Developmental detail in these models is usually minimal and consists of calculating canopy LAI and growth of general plant components of leaf, stem, roots, and seeds. Often these models have quite accurate grain yield predictions for variable environments and cultivars.

Phenology modeling has been one of the most successful components in existing wheat simulation models, and the ability to simulate genotype phenology across a broad range of environments is quite reliable. Many alternative approaches are available for use in predicting phenology, and approaches differ in input requirements and number of developmental stages simulated. All models are based on the thermal time approach (with the many variations that exist), with some emphasizing the role of vernalization and photoperiod (e.g., DSSAT, AFRCWheat2, Sirius) more than others. One area of divergence in phenology submodels is whether leaf number or strictly thermal time is used to estimate the time interval between developmental stages. The AFRCWHEAT2, Sirius, MODWht3 (Rickman et al., 1996), and SHOOTGRO (McMaster et al., 1992b; Zalud et al., 2003) models are based primarily on the leaf number approach, while the others use the more common approach of strict thermal time.

Almost all models do not explicitly consider the phenological responses to water deficits (and usually nutrient deficits) for most, or all, developmental stages (McMaster et al., 2009). Exceptions include the SHOOTGRO model

and the PhenologyMMS decision support tool (http://arsagsoftware.ars.usda.gov), where the number of leaves or thermal time between developmental events from emergence through maturity is adjusted due to water and N levels.

Beginning in the mid-1980s, some research efforts directed greater attention at incorporating the developmental concepts discussed in this chapter into process-based simulation models (e.g., leaf appearance and tillering) and exploration of canopy architecture. Developmental processes other than phenology have been incorporated to varying degrees in whole-plant simulation models. The AFRCWHEAT1/2 model added two interesting components generally missing in existing wheat models at that time: a population ecology element and greater developmental detail derived from European scientists. For example, detailed tillering and leaf dynamics (e.g., appearance, growth, and senescence–abortion) and the effect on canopy LAI were simulated and then used to estimate biomass.

Simultaneously and independently another effort was underway in the US that resulted in the developmentally driven SHOOTGRO (McMaster et al., 1991, 1992a,b; Wilhelm et al., 1993; Zalud et al., 2003) and MODWht3 (Rickman et al., 1996) models. SHOOTGRO is slightly more developmentally detailed than MODWht3, but less detailed in the root system and simulating biomass production. SHOOTGRO provides the foundation to simulate the development and growth of each morphologically identified shoot (main stem and tillers) on the median plant of up to six age classes, or cohorts, based on time of seedling emergence (http://arsagsoftware.ars.usda.gov). All processes in Fig. 2.2 except for leaf primordia initiation and floret primordia differentiation are simulated. Soil water content determines the thermal time required for germination, and seedling emergence rates are simulated to establish the cohorts. Following germination, sequential developmental events are simulated using the number of leaves produced (e.g., phyllochron) between developmental events up to anthesis, and thermal time after anthesis. SHOOTGRO explicitly includes the effect of water and N availability on all developmental and growth processes. As shoots appear, the appearance, growth or size, and senescence or abortion of each leaf blade and sheath, internode, and spike components on each shoot are simulated. Spike development and growth is simulated by the appearance of spikelets and spikelet differentiation into florets, fertilization of florets, and subsequent growth of each kernel.

The Sirius model has one of the most developed leaf appearance submodels of any wheat simulation model (Jamieson et al., 2007). As with the SHOOTGRO model, the assumption used is that the developmental "clock" from emergence to anthesis is best represented by the rate of leaf appearance and final number of leaves. Based on vernalization requirement and photoperiod sensitivity of the cultivar being simulated and on leaf ontogeny, the final leaf number is determined (Brooking et al., 1995; Brooking 1996; Robertson et al., 1996). This allows for an elegant quantitative description of both spring and winter wheat leaf appearance and integration with developmental events.

Canopy architectural, or functional–structural, modeling for a variety of species has increased dramatically since the mid-1990s, in part a result of faster and low-cost computational resources. Modeling efforts have tended to focus more on the functional aspect of the plant such as simulating the biophysical environment of the canopy and resource allocation, and a model usually requires either "setting" the canopy architecture or relatively simple attempts to create the structure (Norman and Campbell 1983; Grant 2001; Dingkuhn et al., 2005; Evers et al., 2005; Renton et al., 2005). Use of L-systems (Prusinkiewicz 1998) or the phyllochron in many of these models has successfully created the plant architecture. Models such as MODWht3, SHOOTGRO, Sirius, and AFRCWHEAT2 might provide further opportunities for simulating greater canopy architectural detail.

Crop simulation modeling is beginning to benefit from the advent of object-oriented design and programming languages such as C++ and Java. Initial efforts have tended to view the plant

as a collection of objects that equate to leaf, stem, root, and seed components (Sequeira et al., 1991, 1997). Recent attempts have begun to incorporate the phytomer approach of building plant canopies into the object-oriented design that can also be scaled up, or aggregated, into lower levels of resolution, such as the seed component of earlier designs (Drouet and Pages 2007; Hargreaves and McMaster 2008).

LINKING MOLECULAR BIOLOGY AND FUNCTIONAL GENOMICS TO DEVELOPMENT

Since sequencing of the model crucifer *Arabidopsis thaliana* genome (Arabidopsis Genome Initiative 2000), and subsequent work with the model cereal rice (Delseny 2007), data are rapidly emerging on genes and genetic pathways related to a number of developmental processes. The hope is that the conservation of gene content and function from Arabidopsis, rice, and other cereals would provide insight for understanding wheat development. Indeed, it appears this hope has been justified in some instances and a generic model has emerged for some processes and traits. Efforts are underway to transform data from molecular biology into information and understanding on the physiological level. Unfortunately, linkage of molecular biology with many developmental processes has not been well established. Considerable challenges remain for understanding and characterizing the function of a gene, identifying the complex genetic pathways for a process, and determining the environmental effects on gene expression before integration with breeding and whole-plant physiology is successful (Edmeades et al., 2004; White et al., 2004a,b).

One area of notable success has been the elucidation of the genetic controls of the flowering pathway (e.g., Hay and Ellis 1998; Laurie et al., 2004 for barley; Beales et al., 2007), and most recent understanding gained for wheat is thoroughly discussed in Chapter 3. Functional orthologues of many of the genes involved have been identified between Arabidopsis, rice, wheat, barley, and other cereal crops. Although the genetic pathway controlling flowering is qualitatively well established, few attempts have been made to predict the time of flowering for plants in the field based on which loci are present and how gene expression responds to the environment. An effort showing promise is using the specific alleles of the vernalization, photoperiod, and earliness *per se* genes to establish the parameters in predicting wheat phenology in the field (White 2006; White et al., 2008). Earlier efforts using neural networks for flowering time of Arabidopsis may also provide alternative approaches for determining wheat flowering time (Welch et al., 2003).

Incorporation of semidwarfing genes was essential for the Green Revolution, and molecular biology is adding greater insight into the variability and functioning of different semidwarfing genes. Functional orthologues of the *GAI* genes of Arabidopsis have been identified for wheat (the *Rht* genes) and other cereal crops. Some efforts have been made to incorporate this knowledge into wheat simulation modeling of plant height (Baenziger et al., 2004).

While other similar examples could be made of new insights emerging from identifying genes and their function and linking the genes to wheat development and modeling (Fowler et al., 1999), most examples have focused on known genes that appear to have more limited genetic pathways controlling the developmental process. With increasing complexity of the genetic pathway controlling a trait, quantitative expression of multiple genes and their response to the environment currently seems nearly intractable given our current understanding. Some overviews of these challenges are discussed elsewhere (White and Hoogenboom 2003; Edmeades et al., 2004; White et al., 2004a,b; Hammer and Jordan 2007; Yin and Struik 2007).

One area where the linkage between molecular biology and wheat development is poorly understood involves the plastochron and phyllochron. Given the variation among cultivars in these traits, and particularly the difference between spring and winter wheat genotypes, this has considerable impact on our understanding and

predictions of wheat development and the building of canopies by phytomers.

FUTURE PERSPECTIVES

A rich history of research has elucidated the complex and interactive interplay among development, phenology, and growth of individual organs on different shoots of the wheat plant. From this work has emerged the general pattern of wheat development and how development responds to the environment. Knowledge of wheat development has increasingly been incorporated into improving wheat management and breeding. Several challenges clearly remain in furthering our knowledge of development and applying it to improved wheat production.

Simulation models and DSS provide tools for quantifying, synthesizing, and applying developmental concepts to many diverse problems. Increased emphasis on translating current and newly gained knowledge of wheat development into electronic forms should improve the currently limited availability of tools designed to address specific problems. Adoption of these technologies is currently quite low, and barriers to adoption need to be addressed.

Continued development of simulation models and DSS likely will further clarify gaps in our knowledge of wheat development. In particular, mechanisms controlling developmental processes and addressing the ubiquitous genotype × environment interaction will need much greater emphasis to extend the robustness of digital analysis and modeling. Successful linkage of wheat physiology and simulation models with breeding has been hindered by the lack of developmental detail in the models and of ways to address the genotype interaction with the environment. The challenges of incorporating knowledge of mechanisms controlling wheat development gained from molecular biology into physiology and simulation models is a daunting problem, but one worth pursuing.

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