several dynamic forces lead to the elongation of the panicle internode, growth of the stem and expansive growth of the leaf. Vertical growth is controlled by the intercalary meristem. Along with lateral expansive growth of the leaf, the panicle component also grows simultaneously. All these processes are coordinated by a hormone-controlled system of organogenesis. Therefore, it is appropriate to conclude that any adverse climatic conditions prevailing during the dynamic growth process will directly affect crop growth as a whole and consequently, its yield. Among the mineral elements, nitrogen in particular influences the cell expansion process. High nitrogen supply will lead to large leaves. The potential of leaf development is influenced by nutrient supply, light and temperature (Milthorpe and Moorby, 1976). Water stress has a direct effect on cell division and cell expansion (Boyer, 1968, 1970; Lockhart, 1965 a,b). Cell division of plants appears to be less affected than expansion in the higher level of water content but does not cease at lower levels (Milthorpe and Moorby, 1976). There is an immediate effect on cell expansion rate due to inadequate turgor pressure required for the maintenance of cell wall growth (Lockhart, 1965 a,b). Hence, prolonged drought directly affects the crop with reduced photosynthesis, reduced mineral nutrient supply, protein synthesis and other aspects of metabolism, as all these adverse conditions affect leaf area development, stem elongation, panicle growth and partitioning of dry matter in plant parts. It is well established that a very strong relationship exists between the temperature and the water status of the plant. Nevertheless, we also know that for all practical purposes, both these factors cannot be separated. Therefore, a more comprehensive approach would be to study other environmental factors affecting leaf growth. Leaf growth and canopy development are of great interest to the crop physiologist. Efficiency of the crop with respect to leaf and canopy development for light penetration would offer suitable recombination of desirable characteristics in cultivars. A dwarf cultivar with few leaves, greater efficiency of these 2 components in tapping solar energy to a large productive head would offer an ideal plant type to the breeder. Therefore, the challenge to the crop physiologist is to come up with an ideal plant type that combines these desirable characteristics.

PANICLE DEVELOP-MENT AND PRODUC-TIVITY

INTRODUCTION

To understand the physiology of crop growth and yield, a thorough knowledge of the developmental processes is essential. In cereals, panicle development and productivity are the principal factors governing yield potential. Productivity of cereals thus depends on how efficient crops are in the biological conversion of radiation into economic yield at the physiologically critical phase of panicle initiation and development and ultimately, in the partitioning of photosynthates into grains. In sorghum, unfavorable conditions affecting the normal developmental process are reflected in the initiation of the reproductive apex and the formation of florets.

At this juncture, crop physiologists are trying to understand panicle development under stress and optimal conditions during rainy and postrainy seasons, and to relate these to economic yield. This aspect is going to be discussed for different crops before focusing on sorghum.

Production of dry matter, its partitioning between grain and straw, and efficient translocation of dry matter and nutrients to the developing grains is the principal contributing factor for productivity in rice (Sircar, 1977). Some genotypes may have higher photosynthesis, but because the sink number, size and storage capacity is limited, the yield may be less. Sircar (1977) stated that the yield of photosensitive winter rice in India is higher in dry postrainy season than in wet rainy season because of higher solar energy incident on the leaf surface.

The physiological bases of growth and yield in wheat and barley have been studied in some detail. Porter et al. (1950) demonstrated that carbohydrates in the grain are derived mainly from photosynthesis in wheat. Barnel (1938) and Stoy (1965) found that wheat and other cereals contain considerable amounts of soluble carbohydrates at anthesis in the stem, but at maturity, these carbohydrates virtually disappear. In wheat, there is substantial loss in the dry weight of the stem during the most rapid period of grain filling, but stem weight rises again (Evans and Wardlaw, 1976; Austin et al., 1977). That this loss was accounted for partly by the stem may be a reflection of the balance between the demand exerted by the grain and the supply from the assimilatory organs. To overcome this problem, a reduction in accumulation of stem reserves and a progressive increase in the proportion of assimilates accumulated in grains is desirable (Evans and Wardlaw, 1976). Sink limitation is as equally important as source limitation in determining grain yield (Evans and Rawson, 1970; Bremner and Rawson, 1972). It was observed in wheat

that the lowest florets are linked directly to the main vascular supply of the spi[?]let, and they are in a favorable position to receive better supplies of assimila[?] for good seed setting (Hanif and Langer, 1972). Under unfavorable conditio[?] the situation is quite different (Langer and Dougherty, 1976). The grainfill[?] period decreased with increase in temperature (Sofield *et al.*, 1977). This has d[?] impact on grain yield. Therefore, researchers advocate that the plant breeder a[?] crop physiologist must consider all 3 stages of cereal life-cycle: vegetative, rep[?] ductive and grain-filling, because the yield operating factors are working in bala[?] with all these stages (Evans and Wardlaw, 1976).

Dogett (1970) and Eastin and Lee (1984) have made a critical review [?] literature regarding the control of panicle initiation and flowering in sorgh[?] Developmental morphology of panicles has also been studied in detail (Paul[?] 1969; Goldsworthy and Taylor. 1970; Lee *et al.* 1974; and Maiti, 1977). Paul[?] (1962) designated the transition of sorghum from vegetative to floral status signalling the end of the first growth stage (GS₁). Lee *et al.* (1974) descri[?] anatomical details of apex transformation and subsequent development up[?] anthesis, growth stage 2 (GS₂). Substantial genetic variability exists in GS₁ an[?] determined by the environment. GS₁ in the insensitive cultivar RS 610 varied fr[?] 27 to 52 days, depending on date of sowing (Paulson, 1962). Rost and Lers[?] (1970) reported that hybrids take less time to reach panicle initiation, more [?] to expand the panicles and a longer grainfilling period than their parents (R[?] and Lersten, 1970). Quinby (1972a) and Quinby *et al.* (1973) demonstrated [?] influence of temperature and photoperiod on the timing of floral initiation a[?] leaf number. Manipulation of photoperiods for flowering in sorghum revealed t[?] GS₃ (grainfilling stage) and far red light at the begining of the dark period [?] photosynthesis hastens floral initiation significantly (Morgan *et al.*, 1977 a,b).

Developmental morphology of the sorghum kernel has been studied by differe[?] researchers (Sanders, 1955; Paulson, 1969; Freeman, 1970). Caryopsis developme[?] at different parts of the panicle in sorghum was also studied by Dickinson a[?] Eastin (1976). Maturity differences among sorghum varieties were considered [?] be due to the differences in response to photoperiod and temperature (Miller [?] *al.*, 1968 a,b; Quinby, 1967). Pauli *et al.* (1964) reported that planting date h[?] great effect on bloom and length of grainfilling. Significant correlation was fou[?] to exist between the duration of GS₃ and yield in sorghum (Dalton, 1967). Emph[?] sis has also been laid on the possibility of improving yield in sorghum by extend[?] GS₃. The decline in GS₃ days was associated with increasing temperature (Eas[?] *et al.*, 1975).

At maturity, the phloem parenchyma at the hilar region becomes blocked w[?] mucilage and pectic componds and forms a black layer that completely shuts [?] translocation of photosynthates from the stem to the grain (Quinby, 1972a; a[?] Giles *et al.* 1975). The development of the black layer is reported to be [?] indication that maximum kernel dry weight has been achieved (Daynard a[?] Duncan, 1969). The appearance of the black layer also indicates maturity (Eas[?] *et al.*, 1973). Grain number and size considered to be important factors in sorghu[?] yield analysis (Stickler and Pauli, 1961; Kambal and Webster, 1966; Beil a[?] Atkins, 1967; Blum, 1967, 1970a). The number of grains per unit area is det[?]

mined by the number of grains each panicle contains. This in turn depends on the number of spikelets.

Studies relating to some cultivars (including hybrids and their parents) and a set of genotypes belonging to different taxonomic groups have been included here in order to give a general idea about the growth and development of sorghum cultivars and their behavior in different seasons. Some of the author's work on the growth and development of sorghum has also been included here to support the conclusions.

GROWTH AND DEVELOPMENTAL STAGES

The growth period of cereals have 3 distinct phases: vegetative, floral initiation and grainfilling. The first or *vegetative phase* is characterized by continual leaf initiation from undifferentiated apical meristem, leaf growth and absence of internode elongation. The second phase or *panicle development*, begins with floral initiation, the internode elongates by differentiation of the apical meristem and ends with 50% of the plants flowering. The third phase, *grainfilling*, is characterized by the development and maturation of grain, with or without the senescence of leaves.

Physiologists working at Nebraska University lay much emphasis on the developmental phases in understanding the relationships between morphology, physiology and grain yield (Eastin, 1972a). Three stages influence the growth and yield of crop in different ways:

GS₁ **Seedling stage**, from the day of seedling emergence to the onset of the reproductive phase, panicle initiation - PI.
1) Establishment of initial root system and shoots producing the panicle (by tillering).
2) Termination of GS₁ determining the total number of leaves on the panicle.

GS₂ **Panicle development**, from the panicle initiation to growth stage 2, anthesis.
1) Expansion of all the upper leaf internodes and all the culms (in case of tillering types).
2) Development and growth of panicle and panicle components.
3) Potential seed number for setting.
4) Continued root growth and nutrient is important as profuse root system is established during GS₂.

GS₃ **Grain filling**, from flowering to physiological growth stage 3, maturity of grain.
1) Development and filling of grains.
2) Seed set and seed size determine the final yield.
3) Length of GS₃ period influences final yield.

Vanderlip and Reeves (1972) have described the developmental and physiological growth phases of sorghum and recognized different developmental stages from 0 to 9 (Table 5.1). The time required to attain different stages varies with the cultivar and season. Following Vanderlip (1972), and also the experience of the author, a brief outline of developmental stages in the vegetative and reproductive organs is described (Figs. 5.1-5.2).

Table 5.1 Developmental stages (Vanderlip & Reeves, 1972) and physiological growth stages (Eastin, 1972a) of sorghum and approximate time required for each stage (unpublished).

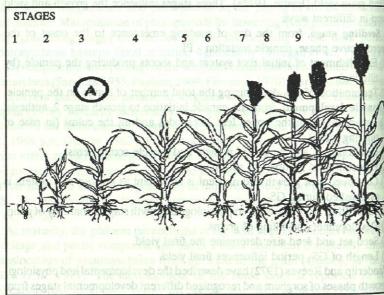| Developmental stage	Identifying characters	Days after emergence	Growth stage
Stage 0	Seedling emergence: coleoptile leaf visible	0	
Stage 1	Three leaf: collar of third leaf visible	5	GS_1
Stage 2	Five leaf: collar of fifth leaf visible	10-15	"
Stage 3	Panicle initiation: growing point differentiation	25-30	"
Stage 4	Flag leaf: final leaf visible	35-50	"
Stage 5	Boot: head extended into flag leaf sheath	40-55	GS_2
Stage 6	Half bloom: half of plants at bloom stage	55-65	"
Stage 7	Soft dough: milky stage	65-80	"
Stage 8	Hard dough: milky stage converted to hard dough stage	75-85	"
Stage 9	Physiological maturity: black hila layer formed at the hilar region of the seed	80-95	GS_3

STAGES

1 2 3 4 5 6 7 8 9

Ⓐ

Figure 5.1 Sorghum development stages (Vanderlip & Reeves, 1972).
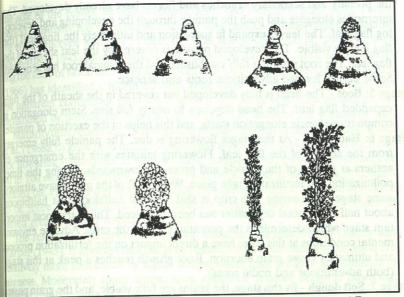

Figure 5.2 Sorghum panicle development stages (Vanderlip and Reeves, 1972).

Stage 0: **Emergence** - At this stage, the seedling shows emergence of coleoptile. The time required for emergence from the date of sowing depends on the moisture content and temperature of the soil. Sometimes crusting and temperature extremes interfere with the emergence of seedling.

Stage 1: **Third leaf** - The appearance of the third leaf is visible in the collar of the first and second leaf. The growing point at this stage is below the ground. The radicle is extended to form the seminal root.

Stage 2: **Fifth leaf** - The appearance of the fifth leaf occurs in the collar of the fourth leaf. By this time, the seminal root has produced some laterals. Two to 3 adventitious roots develop at the base.

Stage 3: **Panicle initiation** (PI) - The vegetative shoot apex is transformed into the reproductive apex, which is demarkated as an abrupt constriction at this stage. Some leaves (6 to 9) are already expanded, while the remaining leaves envelope the panicle meristem. About one-third of the total leaf area is fully developed by this time. One to 3 lower leaves may have senesced. The culm length rapidly increases following growing point differentiation. The root system is wellestablished and seminal root is prominent with profuse laterals. Adventitious roots are well extended.

Stage 4: **Flag leaf visible** - Flag leaf is visible by this stage, and all except 3 to 4 leaves are fully expanded and about 80% of the total leaf area is attained. Up to this stage, the panicle meristems have undergone a series of developments;

the primary and secondary branches and florets have already developed. T[...] internodes elongate and push the panicle through the enveloping and develo[...] ing flag leaf. The leaves expand in succession and ultimately the final leaf ([...] flag leaf) is visible. The developed panicle is covered by the leaf sheath of t[...] flag leaf. The root system is fully established and the seminal root has senesce[...] Some earlier formed adventitious roots also senesce.

Stage 5: **Boot** - The head is fully developed but covered in the sheath of the f[...] expanded flag leaf. The head develops to nearly full size. Stem elongation[...] complete, peduncle elongation starts, and this helps in the exertion of panic[...]

Stage 6: **Halfbloom** - At this stages flowering is due. The panicle fully emer[...] from the sheath of the flag leaf. Flowering initiates with the emergence[...] anthers at the tip of the panicle and proceeds downwards. During this tim[...] pollinization and fertilization take place. When 50% of the plants have attain[...] some stage of flowering, the crop is said to be at halfbloom. At halfbloo[...] about half of the total dry matter has been produced. This is the most imp[...] tant stage which determines the potential yield of the crop. Adverse envir[...] mental conditions at this stage have a direct impact on the fertilization proc[...] and ultimately cause grain abortion. Root growth reaches a peak at this sta[...] (both adventitious and nodal roots).

Stage 7: **Soft dough** - By this stage, the grains are fully visible, and the grain pas[...] through a series of developmental phases. The endosperm changes fron[...] watery fluid to a milky stage (milk comes out if the grain is pressed). Gr[...] formation is rapid and the culm loses weight. Leaves start to senescence. Ei[...] to twelve functional leaves are present by this time. Adventitious roots sh[...] some degree of senescence but nodal roots are active.

Stage 8: **Hard dough** - At this stage, the grain is partially hard. Three-fourths[...] the grain dry matter accumulates in the grains. Additional leaves are lost a[...] more adventitious roots senesce.

Stage 9: **Physiological maturity** - At this stage, the black layer is formed at t[...] hilar region indicating the termination of the vascular connection and fo[...] supply to the grain. The black layer starts at the tip of the panicle and procee[...] downwards. The grain has accumulated maximum total dry weight indicati[...] that the crop has attained physiological maturity. Grain moisture content at t[...] stage varies from 25 to 35%. The remaining functional leaves may stay bro[...] or senesce.

Environmental factors influencing phenology

Sorghum is a short day, photoperiodically sensitive plant, but short ea[...] mutations in tropical sorghum in the southern parts of United States have led[...] development of relatively photoinsensitive sorghum adapted to long day temper[...] environments (Eastin et al., 1984). Eastin et al. (1984) have stated that flo[...] induction in sorghum is caused by several factors, including genetics, photoperi[...] and temperature.

The understanding of the control of flowering and growth in sorghum is imp[...] tant, because it relates to grain yield in temperate climates (Quinby 1973, 19[...] Since sorghum has a terminal inflorescence, the number of leaves initiate[...] controlled mainly by the time of floral induction (Sieglinger, 1936). This influen[...]

the size of the plants, its photosynthetic area, and therefore, grain yield. Photoperiod sensitivity has been developed over long periods of time, thereby selecting the right genotype maturity to meet the local season (Eastin et al., 1984). Quinby and Karper (1945) have identified 3 maturity gene loci (Ma1, Ma2, Ma3) controlling the time of floral initiation and bloom in selected milos. Subsequently, Quinby (1966) has identified a fourth maturity gene locus. Quinby (1974) considers that the apparent continuous variation in genetic control of vegetative growth period terminated by panicle initiation is due to an allelic series at the 4 maturity loci.

Maturity differences in different genotypes disappeared under 10-hr days. Miller et al. (1968a,b) grew milo maturity genotypes under 11-hr days in Puerto Rico and got flowering differences of 42 to 64 days, compared to flowering differences of 40 to 100 days at Plainview, Texas at 14 hr days. Miller et al. (1968a,b) demonstrated the effect of day length, showing that overall, tropical sorghum appeared to be more photosensitive than temperate sorghum, and critical photoperiod varied greatly among tropical sorghums.

The response of temperature to floral initiation was observed by Quinby and Karper (1945). It appears that the gene combinations contributing to earliness are relatively more influenced by higher temperatures than are gene combination in lateness. Moderately lower temperature appeared to cause delays in flowering. Several combinations of light duration and quality and phytochrome levels play a role in the mechanism of flowering (Quinby and Karper, 1945; and Lane, 1963).

Most of the sorghum cultivars seem to be quantitatively short day plants. Miller et al. (1968a,b) reported that the flowering of tropical sorghum is delayed when days are longer, i.e., between 11.1 and 12.6 hours.

On the basis of response of sorghum cultivars to day length, genotypes can be classified as follows:

1. Photoperiod-insensitive: Only temperature need be controlled in these cultivars to initiate flowering.

2. Obligate photoperiod-sensitive: In these genotypes, increasing the temperature to overcome the photoperiod requirement is of no help. For this reason, some cultivars grow very tall and produce a large number of leaves.

3. Facultative photoperiod-sensitive: In these genotypes, a part or whole of the required photoperiod can be met by increasing the temperature in these cultivars to initiate flowering.

Different cultivars require some heat units to attain the phenological stages of growth (Table 5.2). Different environmental factors influence the expression of different phenological stages of sorghum as defined by Vanderlip and Reeves (1972; Table 5.3).

Determination of the developmental stages of panicle

The time required for transformation from the vegetative apex to reproductive apex is largely influenced by genetic characteristics and the environment. In general, it takes 25-30 days for 6 to 9 leaves to fully expand. Periodic sampling is required to locate the exact time of panicle initiation and plants are to be uprooted for this purpose. As the reproductive apex at the panicle initiation stage is situated at the ground level, care has to be taken to remove leaves and locating the apex. The expanded leaves should be trimmed. Gradually, the enveloping leaf

Table 5.2 Sorghum phenology expressed in calendar days as well as heat units (HU) during rainy and postrainy season, 1977 (N. Seetharama, personal communication).

| | Rainy season (sown 18 Jun'77) | | | | Postrainy season (sown 26 Oct'77) | | | |
| | CSH-6 | | Local | | CSH-0 | | Local | |
Stage	Days	HU	Days	HU	Days	HU	Days	HU
0	4	125	4	134	6	176	6	176
1	12	445	12	445	13	376	13	376
2	18	642	18	635	19	576	20	591
3	24	845	44	1500	25	735	33	973
4	41	1394	62	2078	47	1300	63	1606
5	47	1591	66	2214	53	1417	69	1727
6	55	1855	76	2501	62	1582	73	1942
7	69	2288	88	2863	80	1988	93	2282
8	77	2523	98	3199	89	2186	10	2250
9	86	2816	112	3356	97	2399	110	2763

HU= heat units, 10°C as base temperature.

Table 5.3 Influence of environmental factors on the growth stages of sorghum (Seetharama, personal communication).

Growth stages	Factors that control it	Factors that determine yield
GS$_1$		
0 Emergence	Soil temperature and moisture.	Growing plants, plants/hill
1 Three leaves	Soil moisture.	Plantings/plant
2 Five leaves	Soil temperature and moisture.	
3 Panicle initiation	Day length, soil temperature and moisture.	Leaves or spikelets/planting seeds/panicle
GS$_2$		
4 Flag leaf	Day length, air temperature, soil moisture.	
5 Boot	Same as (4)	
6 Half bloom	Same as (4)	Seed/panicle
GS$_3$		
7 Soft dough	Air temperature, soil moisture.	Seed size/weight
8 Hard dough	Same as (7)	Seed size/weight
9 Maturity	Same as (7)	Seed size/weight

sheaths should be unfolded and removed with the help of a needle. Care should be taken to remove the tender leaf primordia enveloping the reproductive apex without damaging it. The meristematic apex needs to be seen under a binocular stereoscopic microscope. For a quick observation, a careful longitudinal section

through the pseudostem would expose the reproductive apex. The bulbous appearance of the apex with a constriction at the base indicates that panicle initiation has occured. The size of the apex is about 0.5 - 0.7 mm.

PANICLE DEVELOPMENT

The transformation of the vegetative stage to the reproductive stage is an important phase in life cycle of a plant. The transition from the vegetative apex to the reproductive apex is marked by a change from the tunica dominated (vegetative apex) to corpus dominated growth. In a longitudinal section through the meristem, tunica is the 1 or 2 outer layers of cells. The corpus forms the inner core of meristem. At this stage, cellular activity of the inner corpus layer relative to the outer tunica layer increases to a great extent. Subsequently, cell division at the corpus layer leads to the initiation of primary branches of primordia.

Paulson (1962), Lee and Lommasson (1972), and Lee *et al.* (1974) have studied the ontogeny of the apical meristem and apex transformation from vegetative to floral status in sorghum. During development, primary branch primordia are initiated acropetally in the panicle axis, while secondary and tertiary branch primordia follow a similar pattern. The development of fertile and sterile spikelets was basipetal. The appearance of glume ridges signaled the formation of spikelet primordia. Anthers are differentiated and surround the pistil primordium. Glumes enclosed the stamens and pistils quickly. Localized initiation of the endoplasmic reticulum (ER) resulted in vacuolar formation, which in turn coalesced to form larger ones bounded by a single vacuolar membrane (tonoplast) in the meristem. Cells of the inner corpus were highly vacuolated. Occasionally, circular double membranes representing ER, encircled a portion of cytoplasm which disappeared later. In a more advanced stage of differentiation further dilation between membranes took place. The total number of primary branch primordia during development depended on the available space on the apical dome and the size of apex increased with increase in the duration of the vegetative phase. Both fertile and sterile spikelets were morphologically similar during their early development, but the florets of the latter degenerated as the inflorescence matured (Lee *et al.*, 1974; Table 5.4).

A thorough understanding of the morphological development of the reproduc

Table 5.4 Developmental sequence of panicle components (Lee *et al.* 1974) and developmental stages, GS$_2$ (after Lee *et al.* 1974).

GS$_2$ - Stage	Days
1. Panicle initiation	0
2. Panicle branch primordia complete	7-10
3. Spikelet primordia	10-14
4. Spikelet component differentiation	14-21
5. Bloom	30-36