tive axis involves discerning the growth phases, the effects of genotype a environment. It may provide the necessary information on the nature and inte tance of some complex agronomic characteristics such as grain yield (Bonn 1961).

Downes (1972) and Quinby *et al.* (1973) report genotypic variation in the t required to panicle initiation (PI). The development of the inflorescence described by a number of researchers (Paulson, 1969; Doggett, 1970; Goldswor and Taylor, 1970; Downes, 1972; Lee *et al.*, 1974; Maiti, 1977). Floral initiati and developmental phases are largely controlled by photoperiod and temperat (Caddel and Weibel, 1971; Downes, 1972; Evans, 1960; Leng, 1951; Ross, 19 Quinby *et al.*, 1973). PI takes about 30 to 40 days after emergence, but may v from 19 to 70 days (House, 1980) and 33 to 45 days (Eastin, personal comm nication).

Quinby *et al.* (1973) indicated that higher temperatures (day/night 32/28°C a 32/29°C) delayed PI. Caddel and Weibel (1971) found that photoperiod sensiti signals the end of juvenile stage at 15 days, if 5 leaves have expanded. It assumed that floral initiation takes place when the proper level of floral stimu (flowering hormone) is reached at the growing point after being transported fr the leaves. The observations by Quinby (1972a) indicate that shortening the per of vegetative growth does not necessarily shorten the period of panicle devel ment. Similarly, lengthening the period of vegetative growth does not lengthen period of panicle development. Kassam and Andrews (1975) showed that expos to long days at this time reduced the number of short days required for initiati Water stress delays PI depending on length and severity (Whiteman and Wils 1965).

At this juncture, it is necessary to summarize and describe the developmen pattern of panicle and its components. The vegetative shoot apex is conical p to panicle initiation. The first sign of panicle initiation is the elongation and domeshaped appearance of the apex with a constriction at its base, enclosed a leaf primordium, followed by the appearance of protuberances which are primordia of primary branches. These are first initiated acropetally and spir on the apex and progress downwards to the base. Elongation of primary branc to a certain size is followed by the appearance of secondary branch primordia the distal end of the branch in a acropetal manner (Lee *et al.*, 1974 and Ma 1977). The last branch (tertiary) of the secondary branch bears the spikelets. first and second glumes of each spikelet enclose 2 florets, the lower one is ste and is represented by a lemma. The upper fertile floret has a lemma and pa Two lodicules are placed on either side of the ovary at its base. The androec consists of 1 whorl of 3 stamens. The anthers are attached at the base of the ov by a very fine filament and are versatile and yellowish in color. The gynoec is centrally-placed and consists of 2 pistils with 1 ovule from which 2 feath stigmas protrude. (Lee *et al.*, 1974; House, 1980). Subsequently, the pan internode (peduncle) and the stem internode continue to elongate.

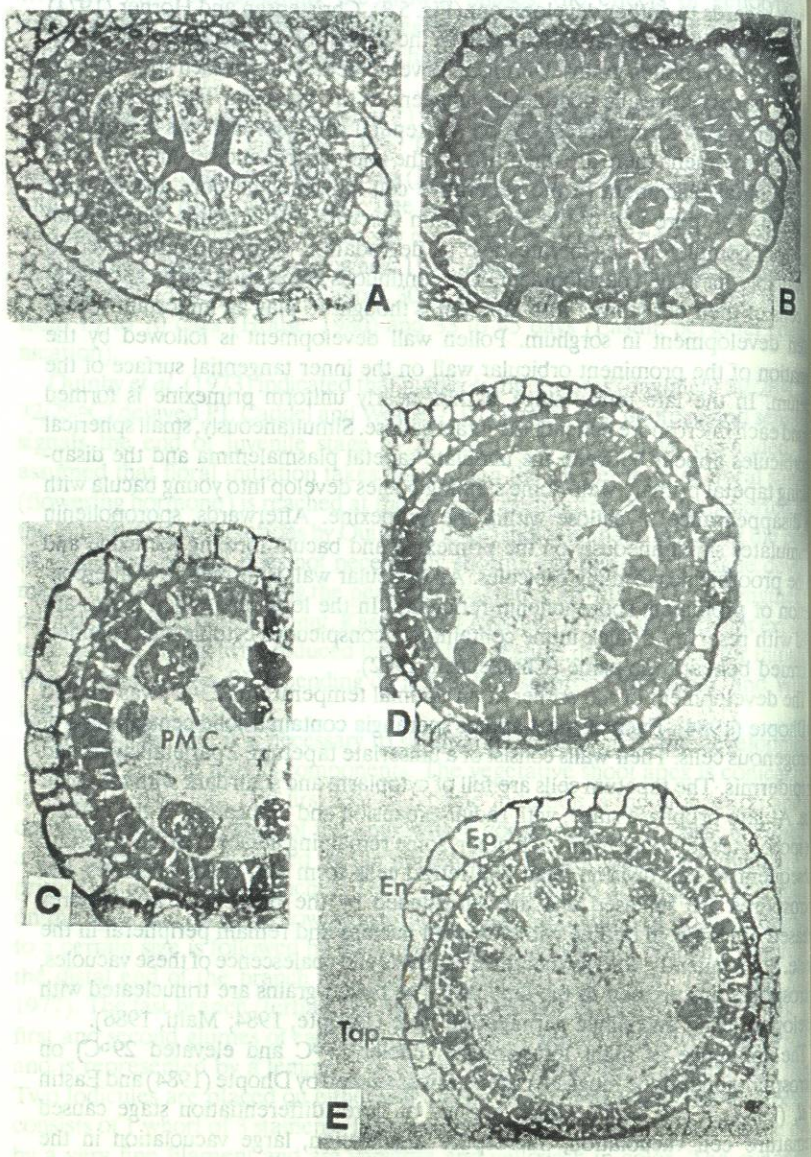
With reference to the development time table of temperate-adapted sorgh at Lincoln, Nebraska, spikelet primordia differentiate about 10 days after pan initiation, floret differentiation proceeds at about 2 weeks and bloom contin

for about 30 to 35 days after PI (Eastin *et al.*, 1984).

With regards to anther development (Fig. 5.3), Christensen and Horner (1974) reported that a strong polarization exists in the anther locule and within individual microspores and pollen grains. During all developmental stages each sporogenous cell and its derivatives lie continually adjacent to the tapetum. The microspores and pollen grains form depressions on the tepetal orbicular wall. As a sequence of polar phenomena there are migrations of the microspores and vegetative nuclei, with an initial placement of the generative cell opposite the pore and its later migration. The pore end of the pollen grain fills with starch grains. The tapetal cytoplasm completely degenerates and its degradation products are believed to be available for pollen development. The continuous association of the sporogenens cells of their derivatives with tapetum is thought to play an important role in pollen development in sorghum. Pollen wall development is followed by the formation of the prominent orbicular wall on the inner tangential surface of the tapetum. In the late tetrad stage, a thin, nearly uniform primexine is formed around each microspore beneath the intact callose. Simultaneously, small spherical proorbicules appear between the undulate tapetal plasmalemma and the disappearing tapetal primary wall. Some staining bodies develop into young bacula with the disappearance of callose within the primexine. Afterwards, sporopollenin accumulates simultaneously on the primexine and bacula forming the exine and on the proorbicules forming orbicules. An orbicular wall is formed by a interconnection of prominent sporopollenin reticulum. In the long run, pollen grains are filled with reserves, a thick intine containing a conspicuous cytoplasmic channels is formed beneath the exine (Christensen, 1972).

The development of the anther at an optimal temperature (23°C) was studied by Dhopte (1984). Each of the 4 anther sporangia contain a solid central mass of sporogenous cells. Their walls consist of a uniseriate tapetum, 2 parietal layers and an epidermis. The tapetum cells are full of cytoplasm and stain dark with toluidine blue. At late prophase stage, with radial expansion and elongation of the anther, the sporocytes separate from each other, some remaining adjacent to the tapetum. Subsequent to cell division, diad and tetrad cells form and callose disolves, the microspores are released and are surrounded by the primexine. Microspores released are wavy in outline with a central nucleus and remain peripheral in the locule. Subsequently, with formation of vacuoles and coalescence of these vacuoles, microspores are pressed to the tapetum. The pollen grains are trinucleated with developed exine and single germination pore (Dhopte, 1984; Maiti, 1986).

The influence of night temperature (cooler 17°C and elevated 29°C) on microsporogenesis and megasporogenesis was studied by Dhopte (1984) and Eastin *et al.* (1984). Cool temperatures applied at floret differentiation stage caused premature cell vacuolation, microspore dissociation, large vacuolation in the tapetum at the late tetrad stage, formation of a callose ring around the tapetum, shrinkage in the anther cavity (14%) and pollen sterility (46%). Elevated temperatures had similar effects, but without callose ring formation around the tapetum. Shrinkage of the anther cavity was increased by 21% with high pollen sterility (60%). Ovule abortion evident in cooler temperature and elevated temperature is associated with the separation of the integuments at the micropylar and the



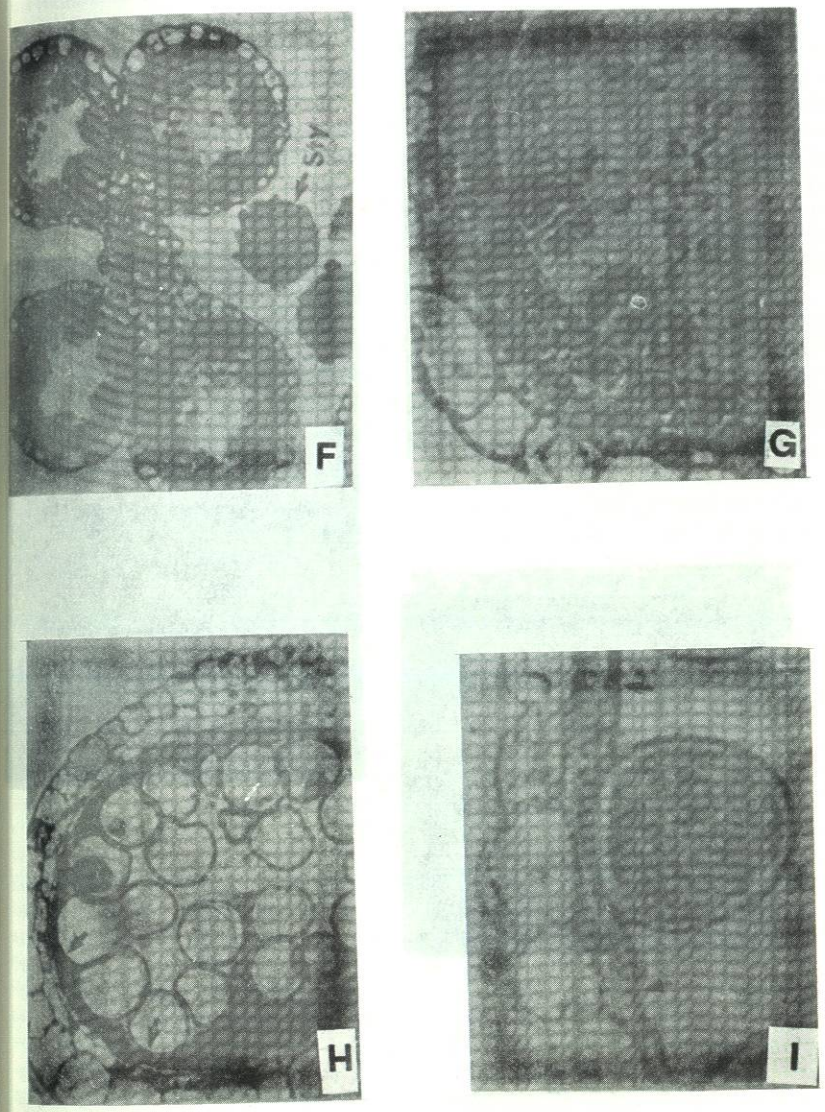


Figure 5.3 Transverse section through anthers, showing: **A)** A microsporangium, its cent cells surrounded by the tapetum, two parietal layers and the epidermis. 470x. **B)** Dough sta of the sporangium with the destitution of the callus; each sporangium cell has its exter surface in contact with the tapetum. 372x. **C)** Callus (C) separating each of the poll mother cells (PMC) in the center of the locullus during the meiotic prophase. 400x. **D)** Di with a new wall, perpendicular to the tapetum, with a predominant callus in the locul (arrow). 375x. **E)** Formation of the triad with 3 disting wall layers: epidermis (Ep), endotesium (En) and tapetum (Tap); all cell maintain contact with the tapetum. 370x. **F)** Loculus (4) showing intact walls and transverse section of the stylus (Sty). 424x. **G)** Loculus (2) and connective tissue (Cn). 604x. **H)** Vacuolated microspore with dense wall and well developed porus (arrow) next to the orbicular wall. 722x. **I)** Fully developed pollen grain still attached to the tapetum (arrow). 2000x.

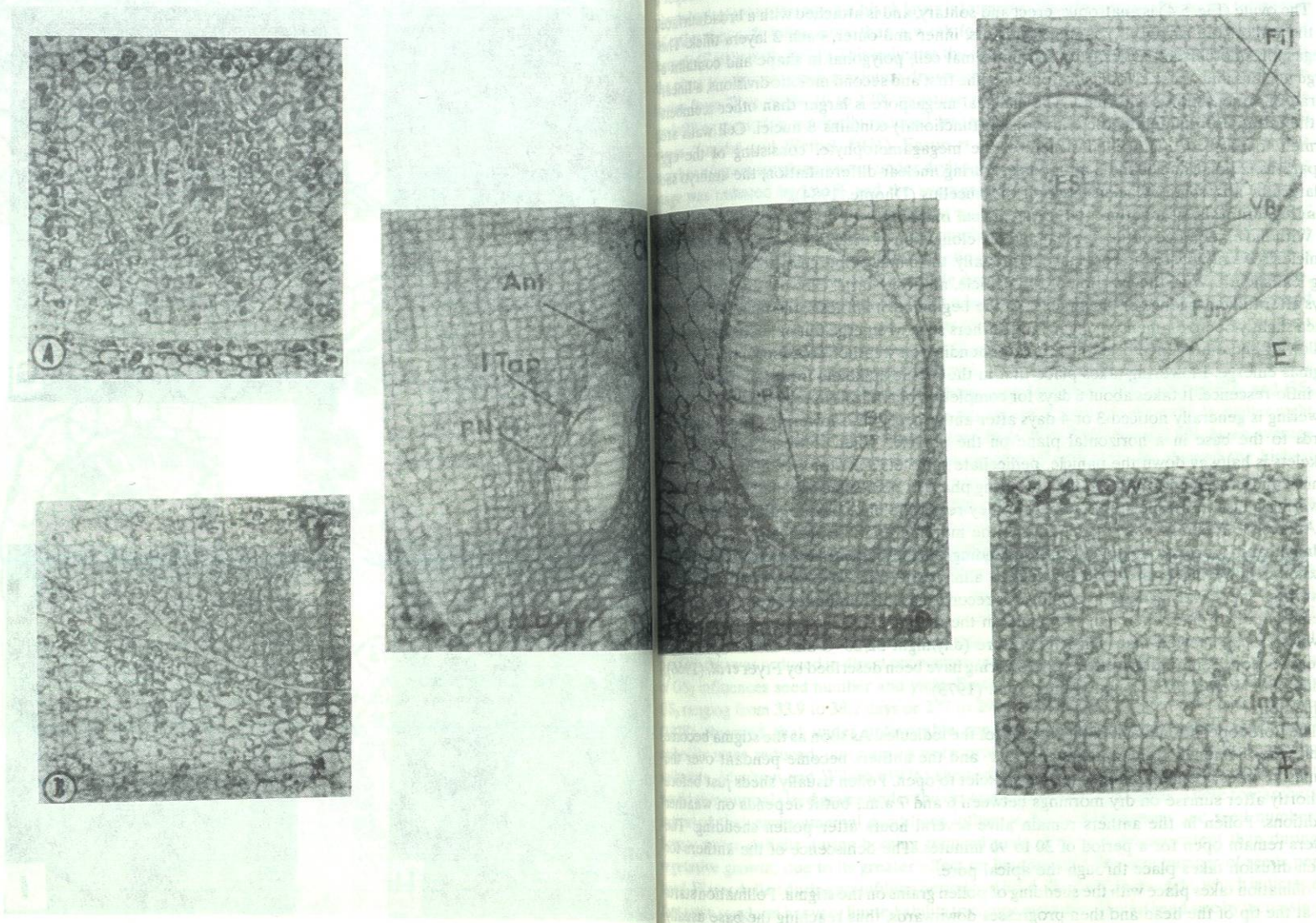


Figure 5.4 A) Functional megaspore (arrow) surrounded by degenerated ones. **B)** Functional megaspore during meiosis II (arrow) inside the embrionic sac. 538x. **C)** Complete embrionic sac with 8 nuclei, 3 antipodes (Ant) at the end of the chalaza (Cha) and 1 polar nucleus (PN) at the center; observe the development of the integument of the tapetum (I Tap) surrounding the embrional sac and the end of the micropilus (ME). 3311x. **D)** Egg cells (EC) and the polar nucleus (PN) at the end of the micropilus. 398x. **E)** Logitudinal section of the ovulus showing the ovary wall (OW) and the upper nuclear tissue (N) localized on top of the antipods of the integuments (Int); observe the arrengement of the cells under normal conditions before fertilization. 323x. **F)** Transverse section of the ovary showing the embrional sac (ES), nucela (N) of the ovulus and ovary wall (OW) connected by the funicula (Fun); observe the vascular sheath (VB) and the tissues of the antera filaments (Fil). 92x.

degeneration of nucellus at the chalazal end. Poorly developed pistils, formation of callo plugs in the pollen tubes and callose depositions in the pollen grains are associated with hi temperature.

The ovule (Fig. 5.4) is anatropus, erect and solitary, and is attached with a broad surfa to the wall of the carpel. It has 2 integuments, inner and outer, each 2 layers thick. T megaspore mother cell arises from a hypodermal cell, polygonal in shape and contain large nucleus and dense cytoplasm. Following the first and second meiotic divisions, a line tetrad of 4 megaspores is formed. The chalazal megaspore is larger than other membe of the tetrad. Subsequently, the embryo sac (functional) contains 8 nuclei. Cell walls a formed to form an eightcelled structure, the megagametophyte, consisting of the e apparatus, 2 polar nuclei and 3 antipodals. During nuclear differentiation, the embryo s enlarges by absorbing adjacent tissue of the nucellus (Dhopte, 1984).

Heading, anthesis, pollination and physiological maturity

With the emergence of the flag leaf and the elongation of the subtending internodes, t panicle grows rapidly to the boot stage. Gradually, the panicle emerges after separating t flag leaf sheath. With the exertion of full panicle, anthesis starts. Flowers begin to open days after full emergence of the panicle. At the beginning of anthesis, the tip of lemma a palea slightly open, filaments elongate and anthers start to emerge out of lemma and pale Following the emergence of anthers, and depending on weather conditions, the feathe stigmas emerge. Flowering takes place first in the sessile spikelets from top to bottom the inflo-rescence. It takes about 6 days for completion of anthesis in the panicle. Maxim flowering is generally noticed 3 or 4 days after anthesis begins. Flowering proceeds dow wards to the base in a horizontal plane on the panicle. When flowering of the sess spikelets is halfway down the panicle, pedicellate spikelets start to open at the top of t panicle and proceed downwards. The flowering phase of pedicelled spikelets overtakes t flowering phase of sessile spikelets before they reach the base of the inflorescence.

Anthesis (blooming) takes place during the morning hours. It normally starts arou midnight and proceeds up to 10 a.m. depending on the cultivar, location and weath Maximum flowering is observed between 6 a.m. and 8 a.m. Wet and cool days del flowering. The flowering date for a cultivar is recorded as the number of days from the da of emergence to date when half the plants in the field are in half bloom (House, 198 Downes (1972) showed that high temperature (day/night 32/28∘C and 35/28∘C) indu floret abortion. Temperature effects on flowering have been described by Fryer *et al.* (196 Caddel and Weibel (1971), and Quinby *et al.* (1973).

Pollination

The floret opens as a result of the swelling of the lodicules. As soon as the stigma becom visible, the filaments of the anthers elongate, and the anthers become pendant over t stigmas. It takes about 10 minutes for the spikelet to open. Pollen usually sheds just befo or shortly after sunrise on dry mornings between 6 and 7 a.m., but it depends on weath conditions. Pollen in the anthers remain alive several hours after pollen shedding. T flowers remain open for a period of 30 to 90 minutes. The dehiscence of the anthers i pollen difusion takes place through the apical pore.

Pollination takes place with the shedding of pollen grains on the stigma. Pollination sta first at the tip of the head and then progresses downwards, thus reaching the base usua 4 to 7 days later (Eastin *et al.*, 1973). A juice that the stigma secretes sticks the pollen gra falling on it. Pollen grains start to germinate on the stigma immediately after it is shed a remains receptive for a period of nearly 10 days. Sorghum is a selfpollinating plant a natural crosspollination varies from 0.6 to 6 % depending on the cultivar, but is usually abo 6%. Pollination for crossing purposes should start soon after normal pollen shedding is o in the morning. Hand pollination might begin around 9.30 or 10.00 a.m. It may extend up to 11.30 or 12.30 in the morning in a foggy morning (House, 1980).

Physiological maturity

Maturity of grain follows a similar pattern to flowering. The development of grains follows a sequence of developmental stages starting from milky, soft dough, hard dough to the final physiological maturity, when a black layer is formed at the hilar region due to the formation of callus tissue. It takes more than a week for the dark layer to move from tip to base of kernels (Eastin *et al.*, 1973). This indicates the cutoff stage for translocation of nutrients from the plant to seed, to attain maximum dry weight. At this stage, moisture content in the grain varies from 25 to 35%; 10 to 12% moisture is good for safe storage. The duration of the grainfilling period is markedly reduced by temperature and under severe environmental stress (Caddel and Weibel, 1971). Eastin *et al.* (1973) and Eastin (1972b) found with a number of grain sorghum grown under dryland conditions for which the average grainfilling stage was reduced by 19.5% and the average yield reduced by 24.5%.

We review here some of environmental conditions that affect GS_2 and GS_3, seed number and final grain yield in sorghum. As seed number is set during GS_2, knowledge of the impact of environmental influences on differentiation and development of spikelets and florets is essential (Wilson and Eastin, 1982). Panicle development is associated with stem elongation, root development and expansion of about 6 leaves in sorghum types found in the USA, and there is a competition between plant parts (Eastin, 1972b). Water stress adversely affects vegetative rather than floral development (Eastin, 1972b; Eastin *et al.*, 1983; Brown, 1978). Lower yields are closely associated with lower seed numbers and lower yields by 25 to 36% were obtained from sorghum held 5∘C above near optimum at night during GS_2 and GS_3 (Eastin *et al.*, 1975). They showed that the duration of GS_2 was reduced 9% by higher night temperature, and increasing day temperature from 29 to 34∘C reduced GS_2 by an average of 17%. The begining of peduncle and elongation of panicle rachis showed the highest sensitivity to water stress affecting seed production (Hultquist, 1973), while Lewis *et al.* (1974) showed yield sensitivity during the boot stage to low water stress. Brown (1978) has showed that enhanced light increased seed number. The ability of sorghum to produce higher seed number is determined at the floret differentiation stage.

Yield is strongly influenced by seed number during the period from floret differentiation to bloom. Ogunlella (1979) demonstrated that the most sensitive period was the floret differentiation (2 to 3 weeks after panicle initiation) where 5∘C above ambient reduced seed number and yields. Production efficiency during grainfill i.e., grain produced per plant per GS_3 day was reduced in direct proportion to seed number reductions. Thus, the duration of GS_3 influences seed number and yield. Eastin (unpublished) recorded in 20 US hybrids GS_3 ranging from 33.9 to 38.2 days or 277 to 298 growing degree units (15∘C base). Brown (1978) observed that under unfavorable conditions, when the number of higher level spikelets were reduced, more grains were produced on the lower branches. By removing spikelets, Muchow and Wilson (1976) showed that more fertile spikelets developed that would give normal sized grains under the expected grainfilling conditions. These researchers indicated that environmental conditions influence floret development and seed number. Severe water deficits during booting reduced grain yield to a greater extent than during vegetative growth, due to its greater effect on limiting head size and number of seeds per head. Water deficit during grainfilling period had little effect on grain weight, which indicated that grain sorghum has very limited ability to compensate for reduced head size by increasing grain weight (Inuyama *et al.*, 1976).

Comparative studies of panicle development of hybrids and their parents (CSH1, All India Coordinated Project Hybrid; 22E, a pioneer hybrid)

Sorghum hybrids usually show earlier maturity, increased plant height, longer stems and leaves, and higher productivity for grain an forage (Kirby and Atkins, 1968; Kambal and Webster, 1966; Quinby, 1973). Embryo weight and early seedling growth of 3 sorghum hybrids showing high, medium and low levels of heterosis indicated that embryo weight of

the highheterosis hybrid exceeded those of other hybrids for seed production (Mil
Atkins, 1979). Greatest heterosis for embryo weight was manifested by the mediumhe
hybrid. This may indicate that factors in addition to embryo size *per se* are involved
expression of heterosis (Miller and Atkins, 1979).

Maiti (1977) studied the time sequence of morphological changes during growth
panicle and its components, from panicle initiation to physiological maturity, the
growth of different parts of the panicle, and the grainfilling period of individual gr
different locations of the panicle. This study helps in understanding the pattern of p
development in sorghum.

Panicle growth:

A comparative study has been described by Maiti (1977) on the growth pattern
panicle and the panicle components in CSH1, 22E and their parents in the rainy s
(Figs. 5.5-5.11). At an early stage, CSH1 showed more or less parental type of grow
a later stage, it showed heterosis for stem and panicle elongation. CSH1 performed
than its parents in accumulating dry matter in the panicle, and its panicle compone
number of primary and secondary branches at all the stages. Hybrid 22E showed a
degree of heterosis for most of the characteristics like stem elongation, internode elong
panicle length, dry weight of panicle and number of primary branches. While the st
hybrid 22E grew faster than that of CSH1, the latter was superior in growth of panicle
ponents. The growth of panicle components in the parents and hybrids reached its
period at 32-36 days after panicle initiation. Later, there was no significant increa
growth.

Development of panicle components:

About 4 days after panicle initiation (PI), primary branch primordia were observ
the tip of the panicle in GS_1. This was followed by a continued formation of primar
secondary branch primordia and new spikelet primordia. These again differentiated
rise to the development of floral parts. Sucessive spikelets started growing at progres

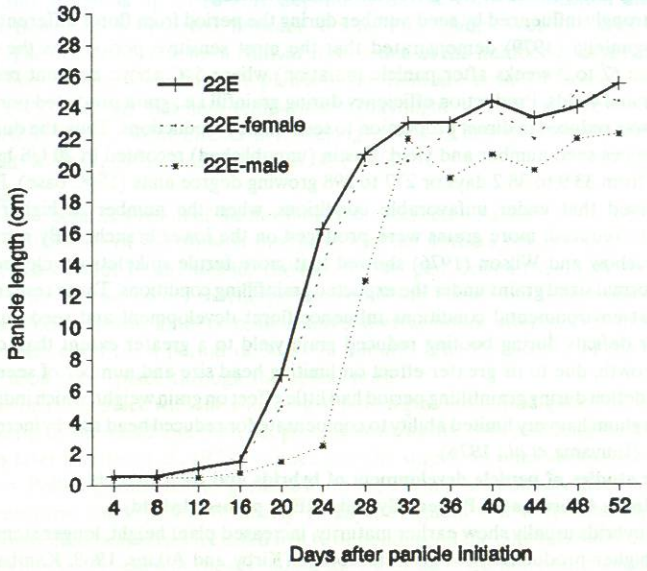


Figure 5.5 Growth pattern of panicle length (cm) in hybrid 22E and its parents in th
rainy growing season 1975 (Maiti, 1977).

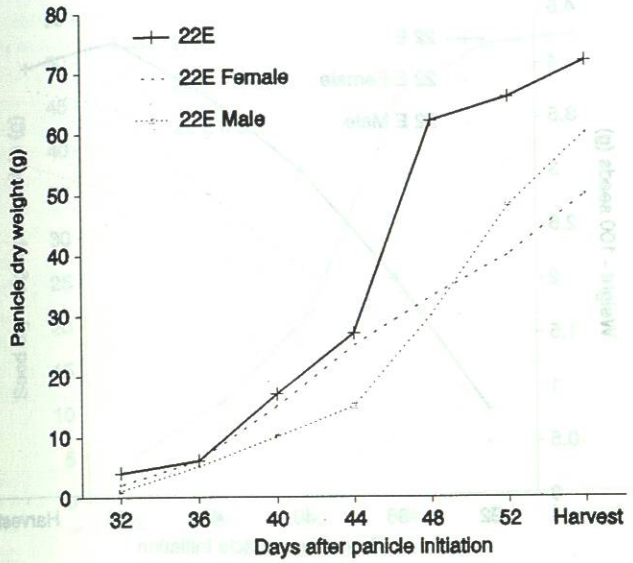


Figure 5.6 Pattern of dry weight increase of panicles (g) in hybrid 22E and its parents in the rainy growing season 1975 (Maiti, 1977).

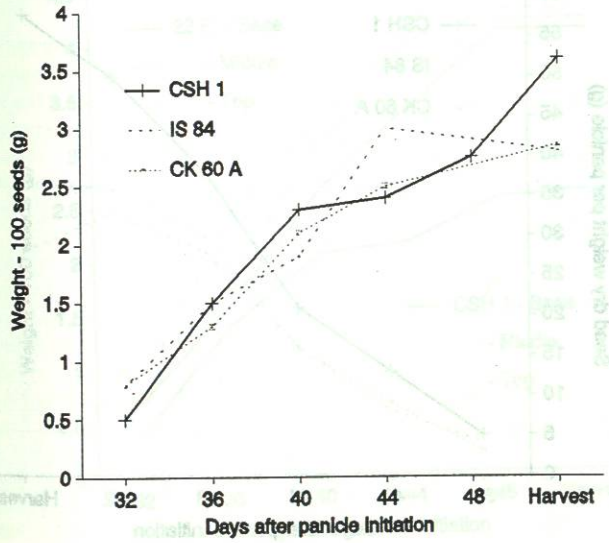


Figure 5.7 Pattern of grain dry weight change (g) in hybrid CSH1 and its parents in the rainy growing season 1975 (Maiti, 1977).

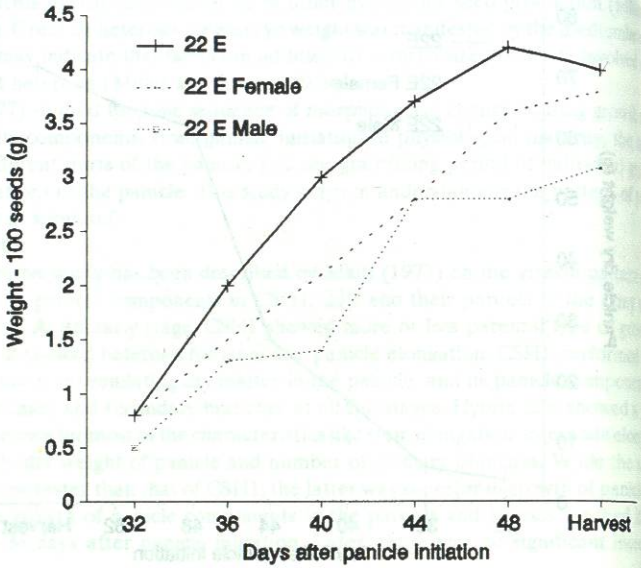


Figure 5.8 Pattern of grain dry weight change (g) in hybrid 22E and its parents in rainy growing season 1975 (Maiti, 1977).

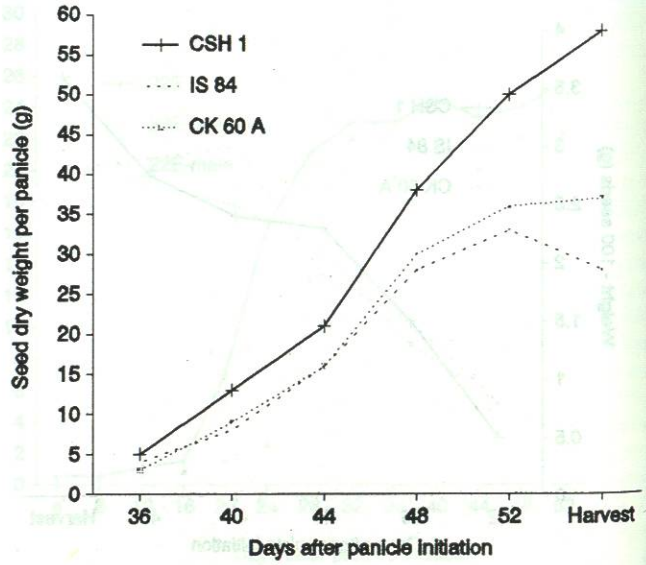


Figure 5.9 Dry weight accumulation of grain per pannicle (g) in hybrid CSH1 and parents (rainy growing season 1975; Maiti, 1977).

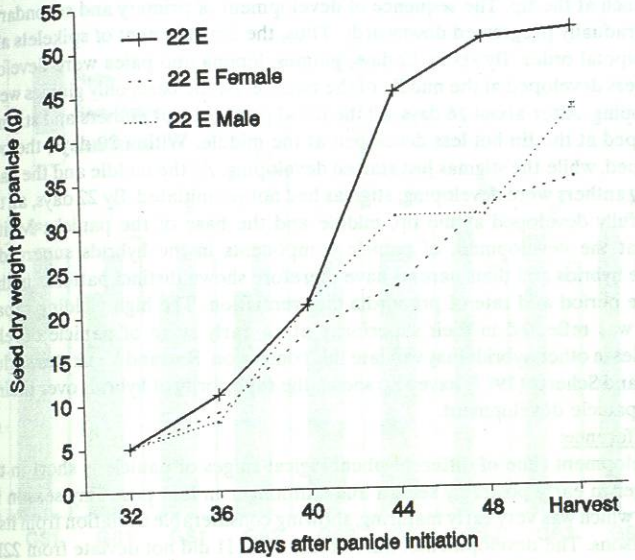


Figure 5.10 Dry weight accumulation of grain per pannicle (g) in hybrid 22E and its par-ents (rainy growing season 1975; Maiti, 1977).

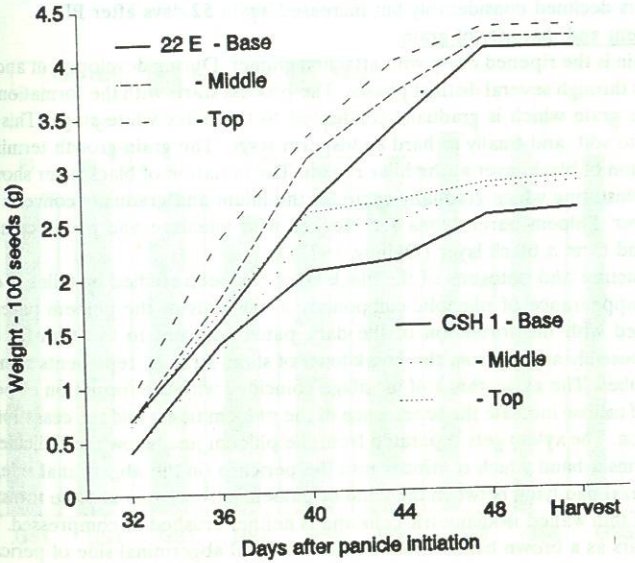


Figure 5.11 Pattern of grain dry weight change (g) at the base, middle and tip of the panicle in the rainy growing season 1975 (Maiti, 1977).