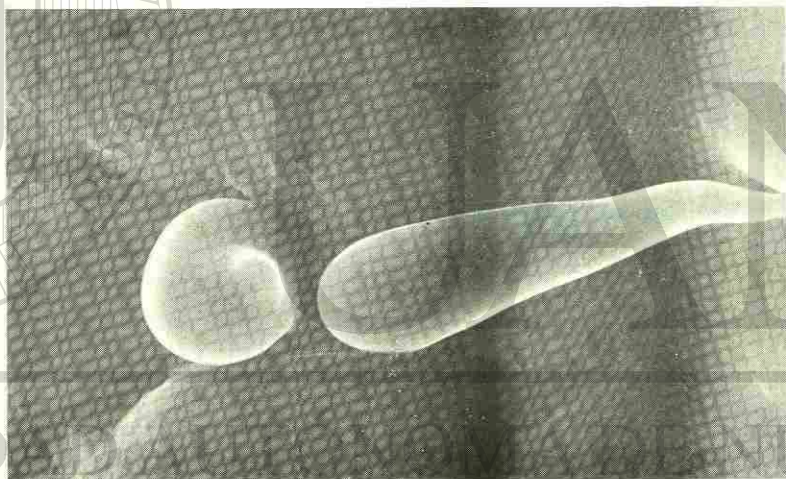


MORPHOPHYSIOLOGICAL TRAITS IN CROP IMPROVEMENT: CASE STUDY - SORGHUM

RATIKANTA MATI



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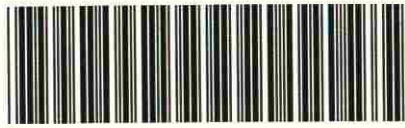
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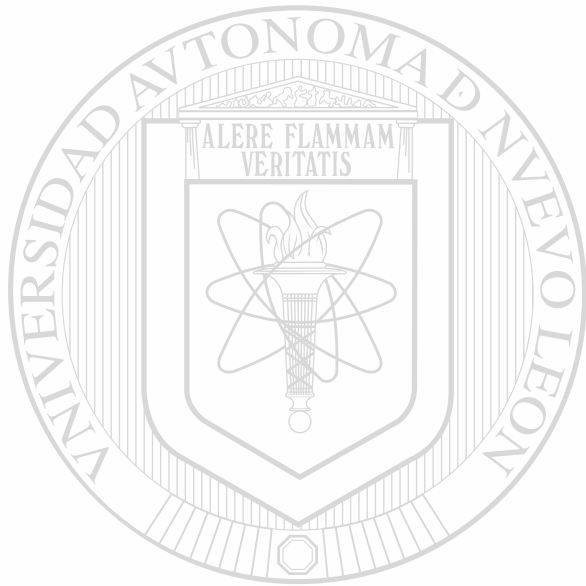
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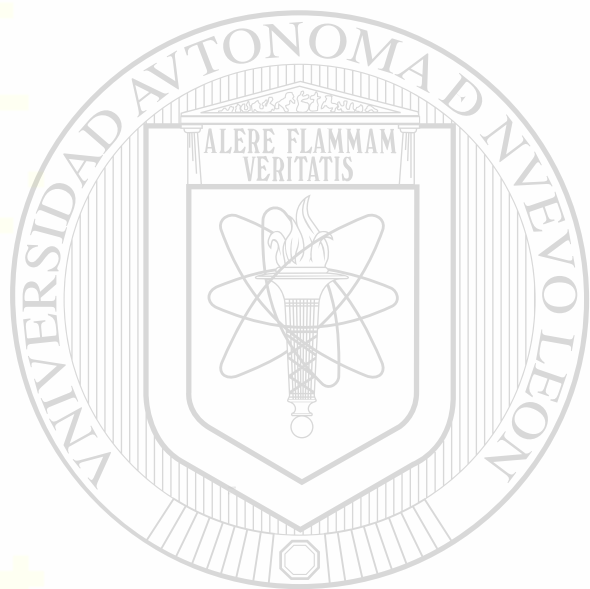


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CASE STUDY - SORGHUM**

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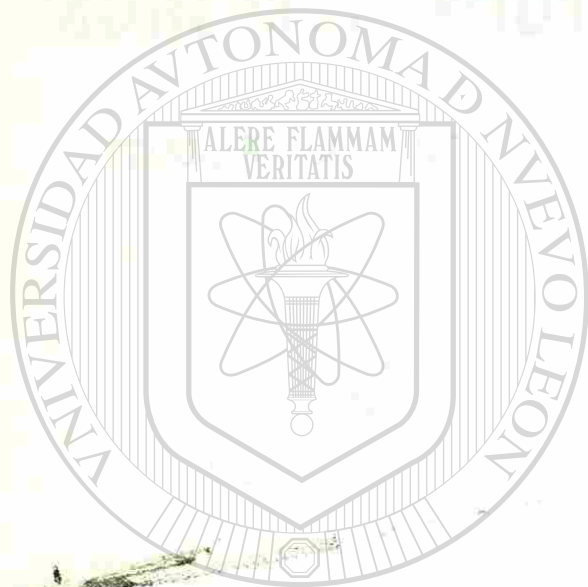
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CITED LITERATURE

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ABOUT THE BOOK

Understanding the process of a plant development morpho-physiological traits in any crop, depends largely on the knowledge of its individual components, namely seeds, seedlings, stems and reproductive meristem. Total productivity is dependent on expression of these plant components which work in harmony. The behavior of these individual components under a variety of environmental conditions is directly reflected in the total productivity of the crop and can be measured quantitatively.

The role of the plant physiologists is to study the vast array of complex functions operating in plant. It is an essential pre-requisite in a crop improvement research program to understand the growth and development of different organs and their constraints under different environments. These factors are considered to determine the structure and thesis of the present book. Although literature is available regarding the growth and development of sorghum, no one book details all these aspects in a concise manner. The main objective of writing this book is to present information of original research by the author and an extensive review of the literature on the subject in each chapter. I have attempted to make each chapter independent; however, there are some repetitions in several chapters. The book is divided into nine chapters.

Chapter 1 is an introductory chapter outlining the sorghum crop, its origin and domestication, the areas under cultivation, its yield potentials and constraints, as well as the research needs.

Chapter 2 deals with morpho-physiological characteristics of seeds. The emphasis has been to show seed morphology related to physical characteristics of seeds and ultimately to the development of seedlings. Factors relating to seed viability, grain germinability and grain weathering are also discussed.

Chapter 3 is concerned with the facets of seedling development the evaluation of seedling vigor and stand establishment traits. Problems of seedling emergence through crusted soil and methodology of seedling resistance and traits related to multiple resistance are also discussed.

Chapter 4 deals with morphology, structure, growth and development of leaf and stem. Distribution of dry matter in different plants organs under different environments is also discussed in this chapter.

Chapter 5 deals with panicle growth and development and its limitation under different climatic conditions. The grain growth pattern, the effect of weather on growth stages and relationship among growth stages and panicle components are also discussed in this chapter.

Chapter 6 discusses the morphology and development of root both in the field and under simulated conditions. As the growth and development of crop is largely influenced by climatic conditions, a general account of crop environments and its effect on sorghum growth and development is discussed in Chapter 7. This includes (1) the general aspects of micro-environments (2) plant responses to physical environments; (3) a review of the effects of water stress on plant function and (4) integrating soil-water-crop environments.

Chapter 8 deals with the mineral nutrition of sorghum and it represents a direct contribution by R.B. Clark, from the University of Nebraska.

Chapter 9 draws inferences of screening techniques for several resistance traits discussed in previous chapters, the research imperatives and evaluates multistress resistance for dryland sorghum crop improvement. It outlines a plan for development of multistress-resistance traits and plant type concepts in sorghum.

This book gives special emphasis to look for genetic variability in morphophysiological traits in sorghum and discusses its possible utilization in crop improvement with special reference to unfavorable conditions. Very few attempts are made in this directions on any other crops.

I believe this book will serve as a guide to students, extension workers and also researchers in sorghum crop productivity. I have attempted to use sorghum crop as a basis for synthesis of the growth and development of other cereals crops. The work done of this crop could be used as a guide for the study of other cereal crops.

R.K. Maiti

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INTRODUCTION

THE SORGHUM CROP

Sorghum is a major source of food for millions of people in the semiarid tropics. In tropical areas sorghum grain is important as food and as livestock feed. The stem and foliage are used as a green crop, hay silage and pasturage. The stems are also used as fuel and building material. In temperate areas, it is a major source of cattle feed except in China, where it is primarily used for food (House, 1980).

Sorghum is used in the preparation of different types of food, and an unleavened bread is the most common food made from sorghum flour. Sometimes the dough is fermented before the bread is prepared, and the grain is boiled to make a porridge or gruel. It is also used in the preparation of biscuits. Beer is prepared from sorghum grain in many parts of Africa. Besides these products, popped and sweet sorghum which are parched, are also eaten (House, 1980).

The demand for sorghum as a staple food has been growing in recent years. Though sorghum is known for its versatile use, hardness, dependability, stability of yield and adaptability over a wide range of cultures and climates, the adverse edapho-climatic conditions prevailing in the sorghum growing areas of the world limit the crop's production (Swindale, 1980). The crop is often grown on poor soils by farmers who have little resources for control of moisture, the purchase of fertilizers, insecticides and other inputs. Therefore, there is a need for the development of cultivars more adaptable to the adverse climatic conditions of the SAT world (semiarid tropics, Figure 1.1).

ORIGINS AND DOMESTICATION OF SORGHUM

Nothing is known about when *Sorghum bicolor* was first brought into cultivation, but Murdock (1959) stated that, along with several West African Crops, it was domesticated some 7000 years ago. It might have reached India not earlier than 1500 BC and China by AD 900. Cultivated sorghums were first introduced to the Americas and Australia about 100 years ago (Peacock, 1984). Sorghum is distributed in wild forms in Africa and other countries. Mann *et al.* (1983) reviewed this subject. In sorghum, domestication is initiated by allelic changes at only two loci resulting from different selection pressures following the innovation of harvesting techniques. Wild sorghum disperse their seeds by the breakage of nodes (due to the absence of an abscission zone along the rachis, panicle or at spikelet nodes) with the subsequent scattering of the seeds. The essential step adopted in domestication was the harvest of the whole inflorescence, and the

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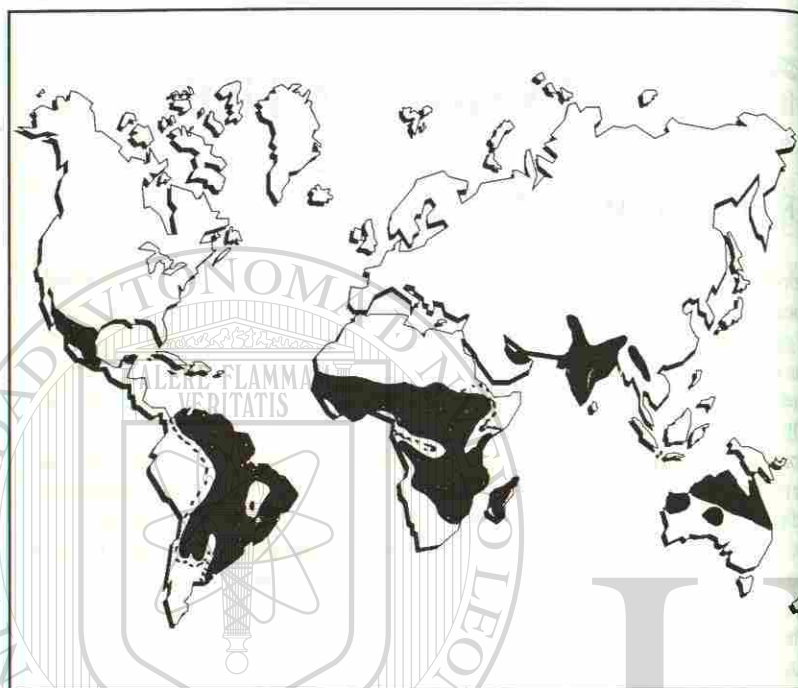


Figure 1.1 The semi-arid tropics, SAT (in black; ---indicates undemarcated boundary)

utilization of the grain for seed. Therefore, scattering is an undesirable characteristic. The types in which panicle components, rachis, panicle branch spikelet node remained intact had selective advantage for domestication. With a short time, this recessive characteristic remained fixed to complete the process of domestication (Mann *et al.*, 1983). The domestication process continued several thousand years. Continued artificial selection increased diversity in crop plants.

Several authors explain the center of origin of sorghum from African countries (Vavilov, 1951; cited by Mann *et al.*, 1983), but Harlan and De Wet (1972) use archaeological, palaeobotanical, anthropological as well as botanical evidence believed that the center of origin of sorghum extends from near Lake Chad Africa. These areas represent the diversity and abundance of wild and weedy species as well as a presence of a primitive race of bicolor. Snowdon (1936; cited by Mann *et al.*, 1983) believed sorghum to have separate centers of origin for different types. Mann *et al.* (1983) presented evidence that sorghum evolved and was first domesticated in northeastern Africa in the area north of the equator and east of 10° E Longitude. The present distribution patterns of wild and cultivated races give strong clues to demonstrate the pattern of evolution and domestication (Mann *et al.*, 1983).

AREAS UNDER CULTIVATION

According to an FAO survey in 1978, sorghum is grown in Africa, southwest and southeast Asia, and North and South America, and on 43 million hectares in both tropical and temperate zones. It is the fourth major cereal crop of the world in production (Higgins, 1978). The cultivated sorghums have spread throughout the world, and today it is grown on 47.8 million hectares (FAO, 1982), making it fifth amongst cereals behind wheat, rice, maize and barley. The major production areas today include the great plains of North America, Sub-Saharan Africa, northeastern China, the Deccan plateau of central India, and Argentina. The potential grain yields of sorghum are similar to those of other cereals in excess of 14,000 kg/ha (Pickett and Fredericks, 1959; Fischer and Wilson, 1975). Sorghum has achieved importance primarily due to its adaptability in arid and semiarid tropics. Average yields in the developing world are near 1000 kg/ha ranging as low as 660 kg/ha in Africa to as high as 3127 kg/ha in Latin America (Peacock, 1984). The global ecological zone for sorghum extends from the humid forest zone near the equator to the deserts of the arid and semiarid tropics. The rainfall characteristics and moisture availability for SAT regions have been compiled and published by the International Crops Research Institute for the Semiarid Tropics (ICRISAT) (Virmani *et al.*, 1980). In Africa, sorghum is grown in 14 million hectares of the drought-prone countries, extending across the full width of the continent between 10° and 20° Latitudes (Motha and Sakamoto, 1979). This area is bounded on the north by the Sahara desert and sorghum is the major food crop in many of these countries. The average grain yield is only 720 kg/ha. In Asia, sorghum is grown on 20 million hectares with yields less than 660 kg/ha. In India, sorghum is the third major cereal with approximately 14 million hectares of which about 50% is cultivated after the monsoons on stored soil moisture. During the rainy season, sorghum is mostly grown as an intercrop with pigeon pea. The area under sorghum crops is on increase from the present 2.5 million hectares. The yield per hectare is 2.4 ton/ha. In Latin America, sorghum is intercropped with other cereals like pearl millet, maize and a number of legumes.

YIELD POTENTIALS AND CONSTRAINTS

Sorghum is a subsistence crop and is frequently grown by small farmers with few inputs under rainfed conditions. The risk involved in making inputs for fertilizer and pesticide are high. In these circumstances, the small farmers of SAT need cultivars which are stable and resistant to different biotic and abiotic stress factors with yields consistently higher than traditional cultivars under traditional management. There are vast differences in sorghum production in different parts of the world, the average ranging from 500 to 1000 kg/ha in tropical countries, and 1500-3000 kg/ha in temperate areas (House, 1982). These differences are due to variability in distribution of dry matter in the plant itself, responses to environments with different levels of stress, and different biotic factors like pests, diseases

es, *Striga* and birds. The crop is being pushed into new environments, especially in marginal areas for maize and on acid soils. In México, where maize is the principal crop, the area under sorghum is gradually increasing for its adaptability (Maiti, unpublished). To improve sorghum production, different ways to incorporate several traits into elite breeding stocks are needed, as well as a better understanding of the plant and its environments. Commercial cultivation of F1 hybrids has contributed substantially to increase sorghum production in many parts of the world. There is a need to introduce high yielding varieties and hybrids with resistance traits in SAT areas where conditions of moisture, temperature, nutrients and other soil factors are limiting and vary considerably from place to place.

A survey was made to investigate yield reducing factors in different sorghum growing regions (Peacock, 1980; Table 1.1). Drought, crop establishment and birds appear to be the major limiting factors in sorghum crop production.

Problems differ in intensity in different environments. For example, shootfly is a major pest on sorghum in India and several African countries, but it is not a problem in the USA, where greenbug is a major insect problem. Therefore, research priorities for sorghum vary with the problems faced by a particular country. House (1982) outlined the priorities of research for the sorghum crop at ICRISAT in India. In his opinion, the main objectives of research are to develop a diverse array of agronomically stable elite varieties and hybrids in a range of maturity with good food quality grain, and with resistance to a number of important pests and diseases, and to *Striga* and drought. The priorities need to be changed with the gravity of the problems in different countries. For example, *Striga* and downy mildew, which were of less importance earlier, are now of great concern in India. The crop growing conditions in SAT are harsh and the farmers are generally poor. In order to maximize production with limited resources in this area, there is need for stability of production including resistance for important yield-limiting factors.

Table 1.1 Most serious problems limiting Sorghum production in countries of SAT (Peacock, 1980).

Countries *	A	B	W	B	O	C	E	G	H	I	K	W	L	M	N	R	P	S	D	T	U	V	Z	TOTAL
Drought	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	14
Stand establishment	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	8
Soil fertility	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	5
Photoperiod																								1
Weeds	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	4
Intercropping																								1
Yield																								3
Grain quality	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	4
Stability																								3
Adaptability																								3
Earliness	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

* Australia; Bangladesh; Botswana; Brazil; Cameroon; China; Ethiopia; Gambia; Ghana; India; Kenya; Malawi; Mali; Mauritania; Niger; Nigeria; Pakistan; Senegal; Sudan; Tanzania; Thailand; Uganda; Upper Volta; Zambia.

A team of multidisciplinary specialists should work together to solve these problems in recognized geographically functional regions. They need to find solutions to the specific problems that may or may not be of concern across different adaptation zones. The research needs should be indicated for respective zones (House, 1982). Research priorities have been identified for various zones of adaptation for each geographically functional regions. These are defined roughly by rainfall and length of rainy season (low, intermediate, high; House, 1982):

1. Indian subcontinent
2. West Africa-low-intermediate rainfall
3. West Africa-high rainfall, long season
4. East Africa-Yemens
5. Southern Africa
6. Central America
7. Tropical South America
8. Far East
9. Southeast Asia USSR
10. Mediterranean
11. Oceania
12. Temperate Americas.

Several national and international organizations are involved in sorghum crop improvement research. This also involves sorghum research and training relevant to the developing world. ICRISAT is involved in research and training for semi-arid tropics of the world. INTSORMIL, and US AID program in the USA, provides funds for research both in US universities and overseas institutions. In West Africa, several regional agencies like SAFGRAD, CILLS, Institute du Sahel and ICRISAT are involved in sorghum research. There are several problems that limit sorghum crop development and productivity as a whole. Stand establishment and drought is an area of high priority. Germplasm and breeding materials need to be evaluated for resistance to disease and pests.

RESEARCH NEEDS

Cultivars tolerant to major limiting factors with stable yields and requiring few inputs will be acceptable to the poor farmers of SAT areas, therefore, the identification and development of resistant cultivars is essential (Table 1.2). There are

Table 1.2 Traits of economic importance in the sorghum improvement program (House, 1982).

1. Yield & Stability
 - a) Genotype x management; genotype x environment; resistance to hazards (see 3)
 - b) Yield potential
2. Quality
 - a) Traditional concepts
 - b) Food preparation and taste
 - c) Nutrition: high lysine, protein content
3. Resistance
 - a) Insects: stem borer, shoot fly, midge, head bugs
 - b) Plant diseases: grain molds, stalk roots, downy mildew, witchweed
 - c) Environmental stress: water, heat, cold, nutrition.

several factors which determine plant productivity in the arid and semi-arid tropical regions. The total production of a crop is productivity multiplied by the quality that represents the limiting factors (Elston, 1980). The productivity of the crop is the yield of plants expressed per unit of some factor that limits production. Therefore, we need to understand the ways in which several factors affect crop development. Attempts should be made to identify resistant genotypes at different phenological stages of the plant. A search needs to be made to identify lines showing multiple resistance to major yield-reducing factors (Maiti, 1981). House (1982) stated that a major thrust of research in SAT is to help the poorer of the farmers working in harsh environments with limited resources. Another thrust is in areas where agriculture is developing and again another in areas where agriculture is highly developed. Sorghum being one of crops of small farmers, attention should be directed on the small farmer of limited means farming his land with few inputs and basically in rainfed conditions (Swindall, 1982). Our job as scientists is not only to develop technology, but to investigate how this technology could be applied by farmers. Research needs to be directed for development of varieties, and adapted for high and/or low input situations.

We should emphasize resistance to major diseases and pests and tolerance to major stress, and ensure that these factors are durable and that yield potential is retained. This involves developing screening techniques for identifying broad-based genetic resistance and tolerance, incorporating them into elite breeding material and screening such material in many situations, including contrasting levels of farming.



SEEDS

2

INTRODUCTION

A healthy seed with good genetic constitution for larger yield and resistance to insects and diseases is a major target of the plant breeder. The growth and vigor of the seedlings are inherent seed traits. This article deals with seed as part of the panicle.

Seeds are borne on the panicles on raceme branches. The panicle varies in length from 4 to 25 cm and is 2 to 20 cm wide. It may be short, compact, loose or open, composed of a central axis which bears whorls of primary branches on each node. Each primary branch bears secondary branches which in turn bear spikelets (Fig. 2.1, 2.2). House (1980) described a sorghum panicle as an inflorescence, which is a raceme consisting of spikelet(s). They are of two types: one sessile and the other pedicellate. The terminal spikelet is a sessile spikelet (Fig. 2.2). The number of nodes in the raceme varies with the genotype.

Sessile spikelets. The sessile spikelets differ in shape from lanceolate to ovoid, and are sometimes depressed in the center. They are green at flowering, but change into purple, black or the color of straw at seed maturity. Glumes enclosing the seed and also the ovary are intensely hairy to glabrous. They are hard and have nerves. Some genotypes possess very thin and brittle glumes, while others possess thin, papery ones. The seed is enclosed between the upper and lower glumes. The lower glume is usually flattened and spikelet-shaped, while the upper glume is more convex or boat-shaped. The seed may be enclosed by the glumes or fully exposed, which differs with the genotype (House, 1980).

There are two delicate lemmas. The lower lemma is elliptical or oblong and of the same length as the glume. The upper lemma is shorter and possesses two pistils and three stamens. In some cases, it has awns. A palea and two membranous lodicules are also present inside the floret. The feathery stigmas with short stout styles are attached to lodicules. The anthers are attached to long-thread filaments (Fig. 2.3).

Pedicellate spikelets. These are narrower than the sessile spikelets and are usually lanceolate in shape. These spikelets possess only anthers, but occasionally have a rudimentary ovary and empty glumes (Fig. 2.4).

According to the IBPGR (International Bureau of Plant Genetic Resource, Rome; 1980) the description of panicle is as follows (Figs. 2.1, 2.2, 2.5).

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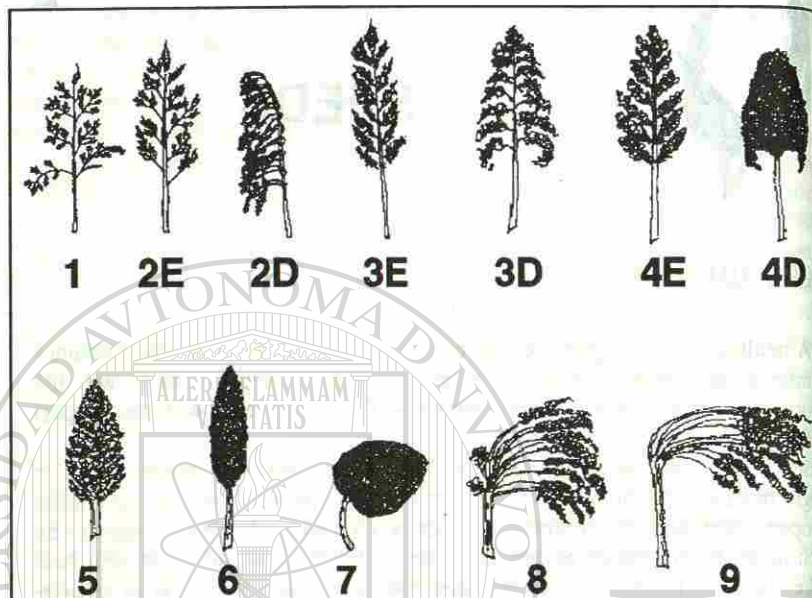


Figure 2.1 Panicle shapes and compactation (see text for description)

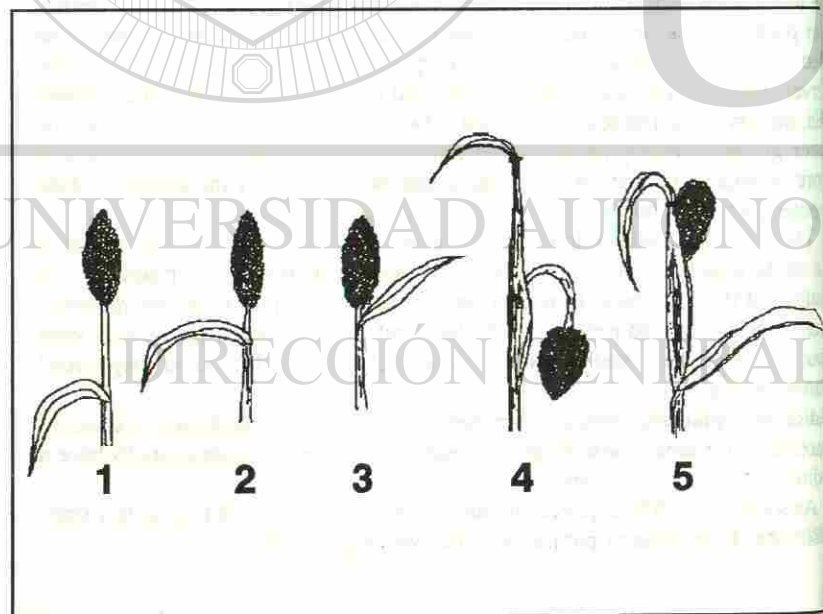


Figure 2.2 Exsertion and peduncle behavior (see text for description)

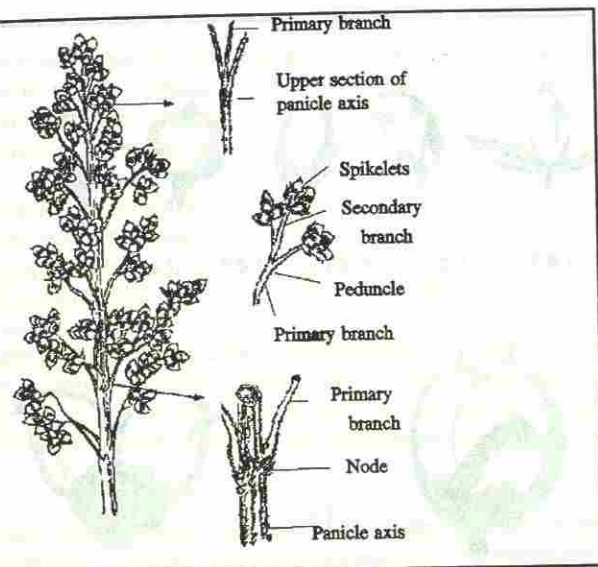


Figure 2.3 Sorghum panicle and its components: a) complete panicle, b) primary and secondary branches, c) spikelets, d) portion of the central axis, and e) portions of the primary branches.

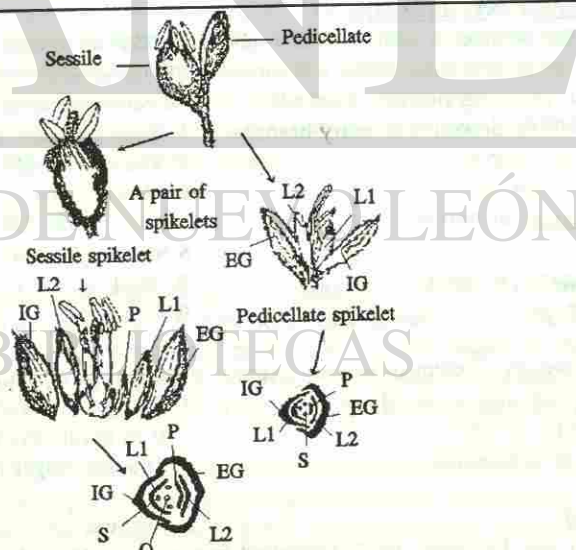


Figure 2.4 Parts of a spikelet: L1 = Lemma 1, L2 = Lemma 2, P = Palea, EG = Exterior glume, IG = Interior glume, S = Stamen, O = Ovary.

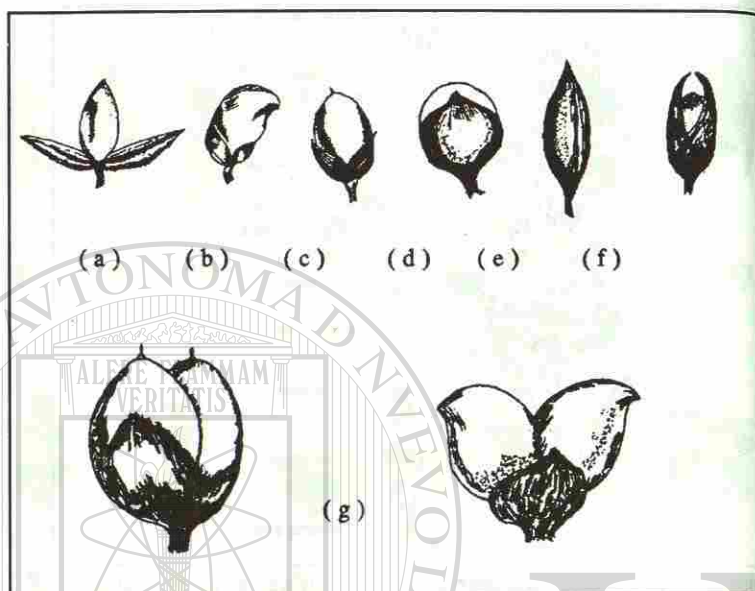


Figure 2.5 Types of seed covering and seed shape. a) uncovered seed, b) 25% covering, c) 50% covering, d) 75% covering, e) 100% covering, f) glume larger than seed, g) double seed.

Head compactness and shape

- | | |
|---------------------------------------------|------------------------------------|
| 1 Very lax panicle, typical of wild sorghum | 2E Very loose erect primary branch |
| 2D Very loose drooping primary branches | 3E Loose erect primary branch |
| 3D Loose drooping primary branches | 4E Semi-loose erect primary branch |
| 4D Semi-loose drooping primary branches | 5 Semi-compact elliptic |
| 6 Compact elliptic | 7 Compact oval |
| 8 Half broom corn | 9 Broom corn. |

Glume Color (at maturity)

- | | |
|--------------------|-------------------|
| W White | S Sienna (Yellow) |
| M Mahogany (Brown) | R Red |
| P Purple | B Black |
| G Grey. | |

Kernel covering (Extent of kernel covered by the glume at maturity)

- | | |
|-----------------------------|----------------------------|
| 1 Very little grain covered | 2 0.25 grain covered |
| 3 0.50 grain covered | 4 0.75 grain covered |
| 5 Grain fully covered | 6 Glumes longer than grain |

Awns

- | | |
|---------|-----------|
| A Awned | L Awnless |
|---------|-----------|

Harlan and De Wet (1972) identified five races in the subspecies *Sorghum bicolor anundinaceum*: 1) Bicolor; 2) Guinea; 3) Caudatum; 4) Kafir, and 5) Durra. Mann *et al.* (1983) have summarized the characters of different races of sorghum

Race Bicolor

Open medium-sized panicles with long clasping glumes; glumes thick and coriaceous with obscure nerves, lower glumes depressed and hairy; pedicellate spikelets persistent; grain elliptic to subglobose, enclosed or almost so by the glumes; pedicels short; glumes and seeds pigmented; grains persistently attached to panicle.

Race Guinea

Panicles long, loose and glabrous, pendulous at maturity, exposing the grain; glumes involute, opening widely, hairy; awns conspicuous; pedicellate spikelets both persistent and deciduous; grains small to medium-sized, biconvex and nearly ovate, some flattened; grain color and nearly pigmented.

Race Caudatum

Panicles medium-sized oblong, dense to slightly open, hairy with stout peduncle with rigid primary branches; sessile spikelet, ovate to elliptic; pedicellate spikelets deciduous; glumes coriaceous, shorter than the large grain, pubescent; grains flat on one side and round to bulging on back; grain chalky white in color or pigmented.

Race Kafir

Panicles erect, elongate, mostly semi-compact, cylindrical; branches and sessile spikelets hairy; glumes at maturity glossy; glumes moderately coriaceous and much shorter than grains; grains broadly elliptic sometimes compressed, flattened or biconvex.

Race Durra

Panicles stiff, dense, compact, ovate to oblong in shape covered with dense pubescence; peduncles often recurved, but occasionally erect; panicle branches short, semi-erect, hairy; rachis elongated or hidden; pedicellate spikelets large, persistent sessile spikelets, obovate elliptic to rhomboidal; glumes coriaceous on lower half and slightly to strongly depressed with central transverse wrinkle, the lower half being strongly nerved with papery tip; lightly pigmented; grain medium to large-sized, biconvex with broad tip and wedge-shaped base.

Table 2.1 gives details of the sorghum collections belonging to different taxonomic groups and their geographic origin.

SEED MORPHOLOGY

Variable seed morphology reflects the genotypic variability of the seed which is important to the breeders. Sorghum seeds vary in shape from elliptic to oval with a pointed beak and a hilum at the base. At the hilar region on the ventral surface of the seed an elliptic depression is seen which demarcates the black layer zone. Usually, the dorsal surface is round, and the ventral surface is slightly flat near the embryo.

Greater genotypic variability exists in the external seed morphology in different taxonomic groups (Fig.2.5). Their morphology differs widely in size, shape, orientation of seed inside the glumes, type of glume, pigmentation and the surface of the seed pattern of the hilar structure, size of the embryonic region, etc.

Most glumes are beset with hairs whose density differs with the genotype. The

Table 2.1 Sorghum collections belonging to different taxonomic groups and geographic origins.

#	IS #	Taxonomic group	Geographic origin
1	13	Nervosum-Broomcorn	USA
2	301	Nervosum-Kaoliang	USA
3	11085	Nervosum	Ethiopia
4	11302	Nervosum	Ethiopia
5	127	Caudatum-Kafir	USA
6	7755	Caudatum-Kaura	Nigeria
7	11574	Caudatum-Durra	Ethiopia
8	3460	Caudatum-Guineense	Sudan
9	8951	Caudatum-Nigricans	Kenya
10	9743	Caudatum	Sudan
11	183	Caffrorum	USA
12	2210	Caffrorum-Roxburghii	USA
13	474	Roxburghii-Shattu	USA
14	7276	Roxburghii	Nigeria
15	7818	Roxburghii	Nigeria
16	6260	Roxburghii	India
17	693	Milo-Kaura	USA
18	714	Bicolor	USA
19	658	Bicolor-Kafir	USA
20	1054	Cernum	India
21	1059	Grass-Grains	India
22	3541	Zera-Zera	Sudan
23	3648	Dochna-Collier	USA
24	681	Dochna-Amber	USA
25	633	Dochna-Honey	USA

a = International classification number.

glumes are either fully covered with bristles or partially covered with hair localized either at the base, at the margins or at the tip. In some cases, they are very large and fully enclose the seed. In some genotypes, the seed has very small glumes at the base, exposing seed to a varying degree. Glumes are morphologically diverse. They may vary from hard to papery, may be easy to separate or closely adhered to the seed and show pigmentation of different shades (Doggett, 1970). The shape of the glumes also differs with the genotype. Their tip may be acuminate to broad, and in some cases, they are fan-shaped with a wavy margin.

The color of the seed varies from pale yellow to deep purple brown with varying shades of red and brown (Doggett, 1970). The pigments are generally present in the seed coat layer. The variation in the distributions of pigments in

different layers has been studied in detail by Ayyangar and Krishnaswamy (1941; cited by Doggett, 1971). The seed coat colors so far observed are reddish brown, light brown, red orange, creamy orange, creamy white and chalky white. The seed coat color is associated with shades or spots of different pigments like purple, black, red and yellow.

Sorghum seed varies in shape and may be oval, elliptical or spherical. The seed may be simple or plump. Twin seeds are also found in some genotypes. The seed shows two pointed outgrowths (stylar bases) at the beak region. The depression at the hilar region varies in size and shape and may be flat or slightly to deeply depressed; it may be narrow or extended laterally, and its shape may be pearl cylindrical, club or irregular.

The proportion of embryo to the seed differs with the genotype. Striation of the dorsal and ventral surfaces are special features and appear sparingly in some genotypes. The surface may be smooth or rough and may show blisterous minute outgrowth beset with minute hair which can be seen only under a dissecting microscope. The embryo surface at the scutellar region shows the presence of longitudinal lines or striations passing towards the beak. Sometimes, the embryo surface resembles the venation pattern of the cotyledon which may be faintly bilobate. The seed surface may show reticulate longitudinal or horizontal striations, crinkled in rare cases. The seed coat may be shining, partly shining or dull. It may be soft, partially hard or very hard.

In order to describe the seed of a particular genotype the following features need to be carefully examined:

- 1. Glumes:** Thick or papery, soft or hard, pigmentation, shining or dull, fully or partially enclosing the seed, adhering to the seed or easy to separate.
 - 2. Seed coat color:** Creamy white, brown or yellow with different color shades, dull, shining or partially shining, soft, partially hard or hard.
 - 3. Seed coat testa:** Present or absent.
 - 4. Seed shape:** Round, oval, elliptic, spherical or flat.
 - 5. Seed size:** Small, medium or large; test weight (100 seeds); length, breadth and thickness (dimensions taken with a seed micrometer).
 - 6. Surface:** Smooth, crinkled, striations, lines, blisters or swellings or any other peculiarities, dorsal and ventral surface round, flat or laterally compressed.
 - 7. Beak:** Pointed, flat or depressed.
 - 8. Hilar region:** Nature of black layer.
 - 9. Embryo surface:** Flat, slightly or deeply depressed or (scutelum surface) faintly bilobed; longitudinal lines or striations or any other peculiarity on the embryo surface; color and hues; length of the embryo in proportion to seed surface.
- Description of seed morphology by the IBPGR system:
- Kernel color:** 1. White; 2. Yellow; 3. Red; 4. Brown; 5. Buff.
- 100 seed weight:** Weight of 100 kernel at 12% seed moisture content.
- Endosperm texture:** 1. Completely corneous; 2. Almost corneous; 3. Partly corneous; 4. Almost starchy; 5. Completely starchy.
- Endosperm color:** W. White; Y. Yellow; S. Sugar.
- Kernel luster:** L. Lustrous; N. Non-lustrous.
- Sub-coat:** A. Absent; P. Present.

Kernel plumpness: D. Dimple; P. Plump.

Seed formation: S. Single; T. Twin.

Distribution of corneous and floury endosperm

Two types of endosperm are found in the seed, corneous and floury. The corneous endosperm is also called vitreous endosperm and is present at the periphery, while the floury endosperm is found in the inner core of the main bulk of the endosperm (Fig. 2.6). Cells in the corneous endosperm are oval to slightly elongated, with compactly arranged starch and protein granules, while the cells in the floury part are much more elongated and broad with loose arrangements of starch and protein granules.

Lateral and dorsoventral sections give an idea about the distribution of the

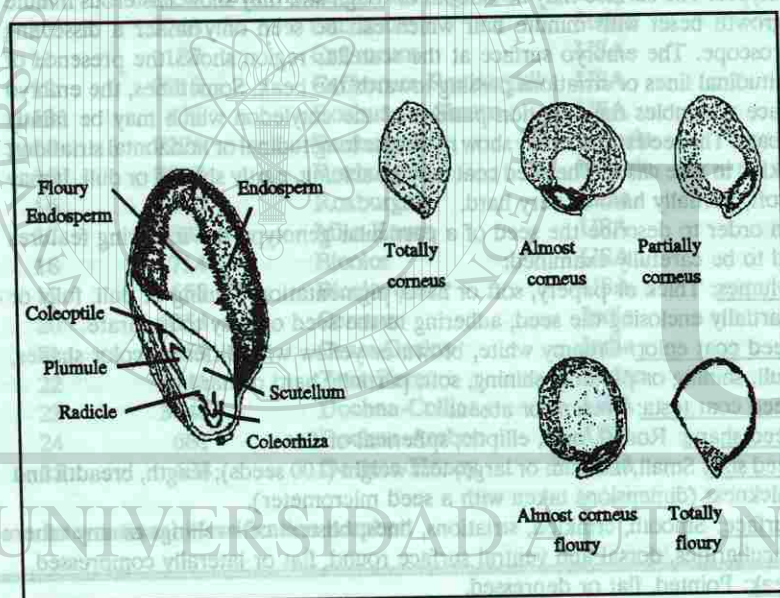


Figure 2.6 Parts of the seed and texture of the endosperm.

components of the endosperm. In the lateral section, the scutellar tissue, along with the embryo, can be seen clearly near the broad hilar region. The pointed end of the embryo is inclined towards the lateral wall of the seed. The corneous endosperm encloses the inner mass of floury endosperm.

The dorso-ventral sections shows the morphology of the corneous and floury endosperms, and of the embryo, as seen under a microscope (Fig. 2.7). The corneous endosperm fully or partly surrounds the floury endosperm, while the floury endosperm is surrounded by the embryo; At some places, it may be narrowed down to a thin layer. The shape of the floury layer assumes different forms of pitchers which may be continuous from the embryo region up to, or near the

base of the hilar region. The shape of the pitchers may be narrow or broad, with a constricted neck. They may assume the shape of a fan or a conical flask, bounded fully or partially by the corneous endosperm. The embryo with scutellar tissues in the dorsoventral section appears pearl-shaped and varies in size in different genotypes. In some cases, the orientation of embryonic leaves and radicle with coleoptile and coleorhiza can clearly be seen.

A close examination conducted on a sizable germplasm collection representing different taxonomic groups evaluated under similar weather conditions indicated good genotypic differences for the intensity of corneousness over floury endosperm. The differences in intensities of floury vs. corneous endosperms allowed an arrangement of the genotypes into the following categories:

1. **Almost the entire endosperm is corneous:** Only a very little floury portion may be present in the center (completely corneous, IBPGR).
2. **Over 50% of endosperm is corneous:** The endosperm is broad (almost corneous, IBPGR).
3. **The endosperm is almost floury:** A thin layer of corneous endosperm may be present which should not exceed 10% of the entire mass which surrounds the broad floury endosperm mass (almost starchy, IBPGR).
4. **More than 75% of the endosperm is floury:** The corneous layer is medium broad (partly corneous, IBPGR).
5. **The whole endosperm mass is floury:** A thin corneous field of the endosperm may be present (full of starch, IBPGR).

DEVELOPMENT OF CARYOPSIS

The caryopsis development of CSH1, a hybrid of the All-India Coordinated Project, was thoroughly studied at ICRISAT. The ovary in longitudinal sections was found to have three distinct regions: epiderm, mesoderm and endoderm.

Epiderm usually had a single layer of well-defined cubical cells, occasionally double layers were also seen. It was followed by a broad mass of homogeneous layers of compactly arranged parenchymatous tissue. The inner mesoderm layers (12-20) were distinct from the outer broad zone of homogeneous tissues, where the cells are multinucleated, elongated, compressed and arranged more or less serially in 6 or 7 layers. This layer was followed by a single layer of larger ovoidal cells, completely differentiated from the outer and inner mass of tissues. Below this, there was a mass of homogeneous tissues of much larger and irregular cells which had broad lumens, and occasionally were compressed (Fig. 2.8).

After five or six days of grain development, the mesocarp cells showed a cytoplasm with condensed nuclei prominent at the center (Fig. 2.9). There was free nuclear division in the cells followed by the formation of a network which fills up the whole cavity, but in a discontinuous way, with large vacuoles here and there. At slightly more advanced stages, an oval mass at the center of the nucellus could be seen in the middle of a wide mesh. This was associated with an increase in volume and gradual filling of the nucellus, which later formed the endosperm.

After eight or nine days, formation of hypocarp was just initiated and that the

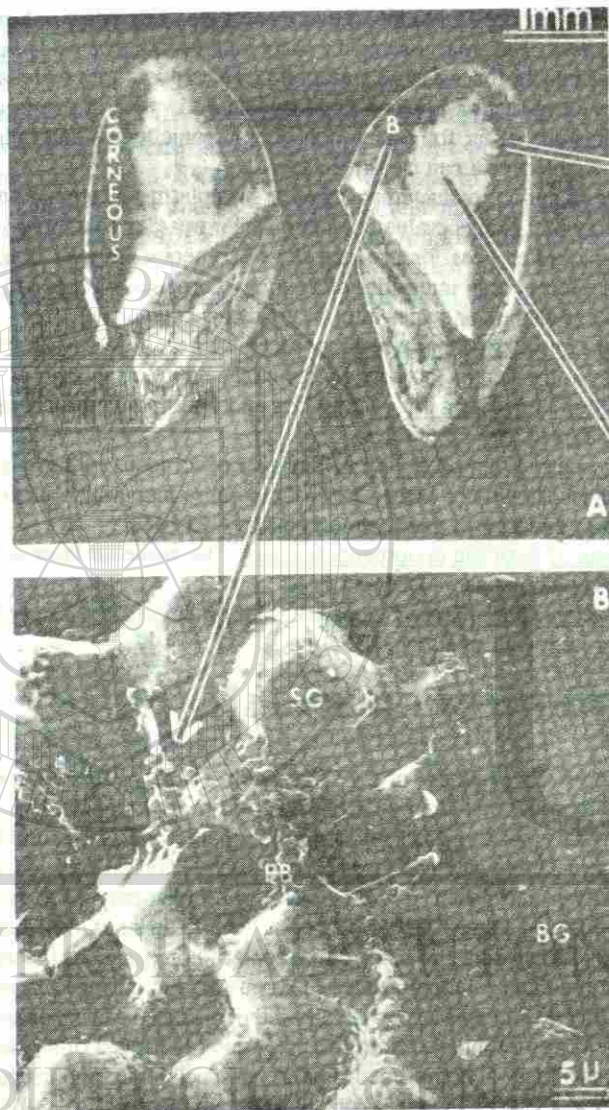


Figure 2.7 Scanning electron microscopic (SEM) analysis of the corneus and flury endosperm of the sorghum seed.
 A) Logitudinal section of the corneus and flury endosperm,
 B) Typical structure of the corneus endosperm with a continuous flury endosperm between the flour and the protein, resulting in a space without air spaces between the starch granules; the corneus endosperm appears extremely dense and vitreous.



Figure 2.7 (Continued)
 C- Transition section with corneus and flury endosperm cells.
 D- The flury endosperm contains air spaces between the starch granules with a clustered and loose appearance.
 SG = Starch granules, PM = Protein matrix, PB = Protein bodies, BG = Broken granules.
 (Courtesy of L. Rooney, Texas A & M University).

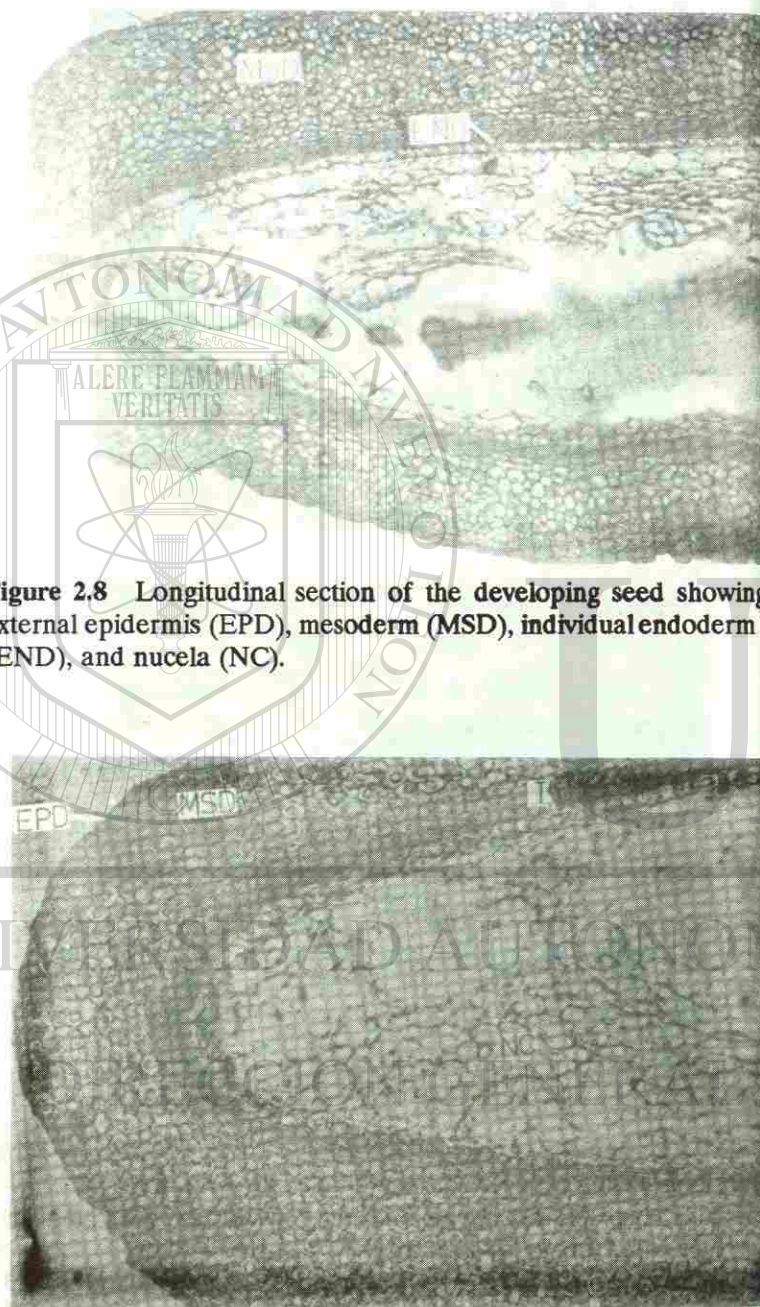


Figure 2.8 Longitudinal section of the developing seed showing external epidermis (EPD), mesoderm (MSD), individual endoderm (END), and nucela (NC).

cuticle was not yet developed. On the upper node, the hypocarp was well developed and the cuticle formed. After 12 to 13 days the aleurone cells were much more developed, and the endosperm cells continued their development with distinct nuclei. The mesocarp cells were rectangular in shape and contained starch granules. Network pattern are formed at different places of the endosperm. Starch cells were not fully formed. After 17 to 18 days, the pericarp was fully developed and epicarp consisted of thick-walled rectangular cells with well developed cuticle. The hypocarp consisted of one to three layers of elongated cells with prominent nuclei. The mid-portion of the pericarp was composed of polygonal cells without intercellular spaces. Starch are profuse in the mesocarp cells. Cross cells and tube cells are also fully developed (Fig. 2.10).

At 20-21 days after flowering the caryopsis was fully formed. The cuticle was fully developed and the epicarp provided with nuclei. The hypocarp consisted of 2 to 3 layers of cells. This zone was followed by seven to eight dense layers of mesocarp cells, and by elongated loose cells. Next, the layers were narrow zones of compressed cross cells and tube cells. Immediately below this layer was a single layer of narrow elongated cells forming the aleurone layer. This layer was followed by compactly arranged smaller cells forming the corneous endosperm of 8 to 10 layers. The middle layer consisted of milky endosperm with many intercellular spaces. The starch grains of the corneous endosperm that surrounded a central core of mealy endosperm were more compact (Fig.2.11). The embryo was surrounded by a tissue of scutellum as the boundary through which it derived its nutrients from the endosperm during development.

Anatomy of mature kernel of seed

The structure and chemical components of a mature seed are of interest to food chemists. In a mature seed, the seed wall is fused with the fruit wall which is a characteristic of monocot seed. About 20-25 days after flowering, the fruit seed, called caryopsis, is fully developed (Fig. 2.12, 2.13). Caryopsis consists of three main parts: the pericarp or outer covering, the endosperm or storage tissue and the germ or embryo. Details of these structures have been discussed by many authors (Rooney and Clark, 1968; Rooney and Sullins, 1977; Sanders, 1955; Sullins and Rooney, 1974, 1975). Glueck and Rooney (1980) have given a detailed account of the chemistry and structure of the grain in relation to mold resistance.

Description of the parts of a caryopsis:

Pericarp:

The pericarp which forms the peripheral boundary of the seed consists of epicarp, mesocarp and endocarp. The outermost layer or epicarp, is made up of 2 to 3 layers of long and rectangular cells, which contain wax and pigments. The hypocarp consists of 2 to 3 layers of cells. This zone is followed by 7 to 8 dense layers of mesocarp cells containing small starch granules embedded in a fluid proteinaceous material within the cell. Mesocarp cells vary in thickness, from a

Figure 2.9 Longitudinal section of a more developed seed showing epidermis (EPD), mesoderm (MSD), testa (T), and nucela (NC).

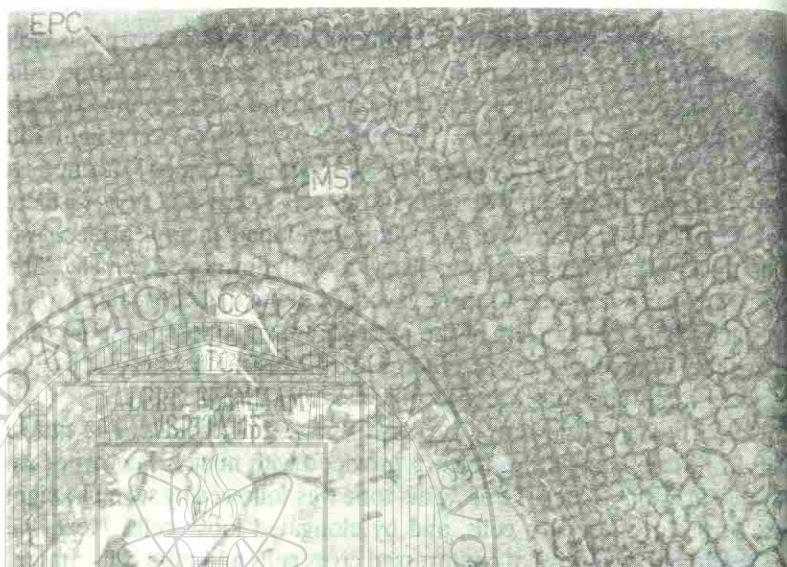


Figure 2.10 Transverse section of a caryopsid (12-13 days after anthesis) showing a well developed epicarp (EP), mesocarp (MS), cross cells (CC), tube cells (TC) and testa (T).

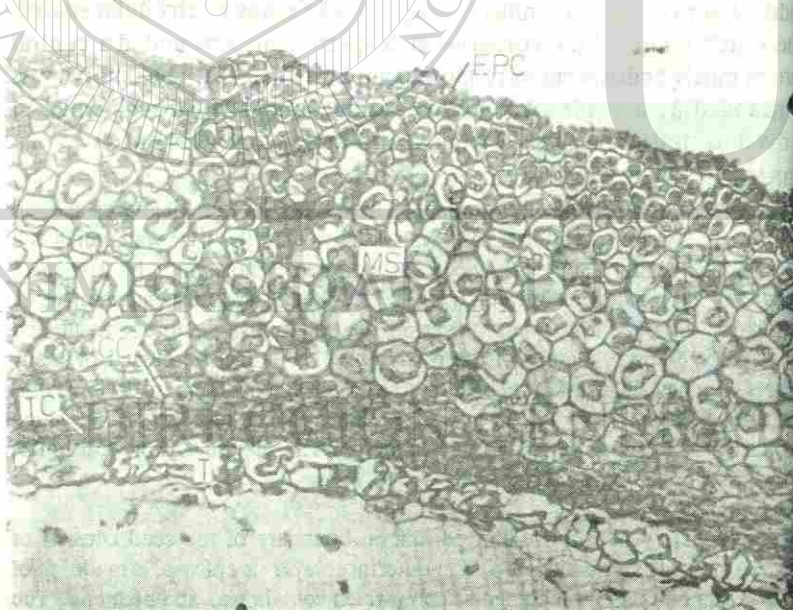


Figure 2.11 Transverse section of a well developed caryopsid showing the epicarp (EP), mesocarp (MS), cross cells (CC), tube cells (TC) and testa (T).

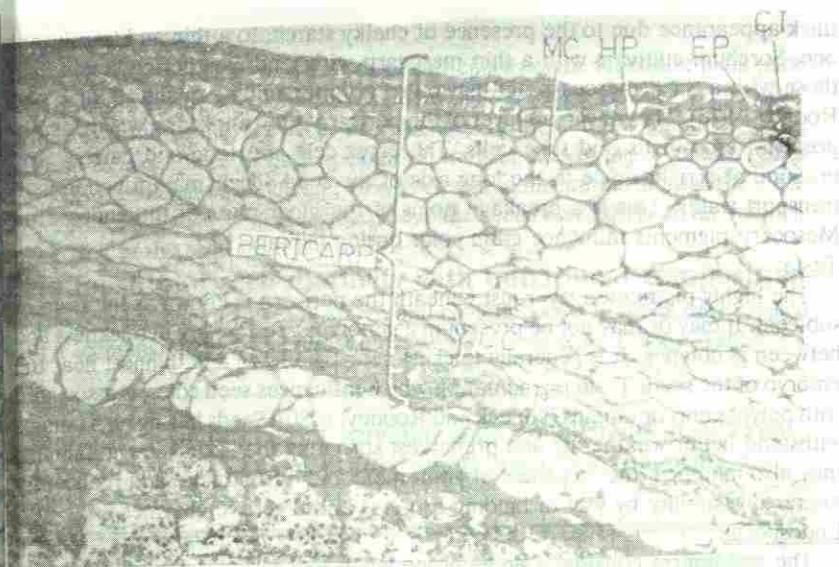


Figure 2.12 Transverse section of a mature caryopsid showing cuticle (C), epicarp (EP), hypocarp (HP), mesocarp (MS), cross cells (CC), and tube cells (TC).

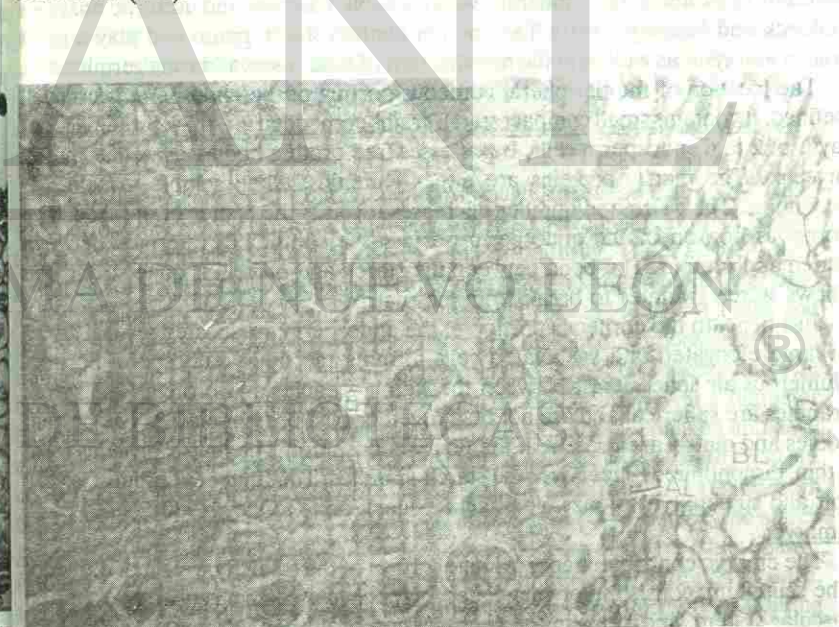


Figure 2.13 Transverse section through the hilar region showing endosperm (E), black layer (BL), cross cells (CC), and aleurone layer (AL).

thick appearance due to the presence of chalky starch, to a thin and translucent one. Sorghum cultivars with a thin mesocarp withstand weathering better than those with a thick mesocarp and have also a better milling quality (Glueck and Rooney, 1976). The innermost layer of the pericarp is the endocarp, which is composed of cross cells and tube cells. The cross cells are long and narrow, and oriented at a right angle to the long axis of the seed. Their main function is to transport water. This is a breakage point of the inner mass of the endosperm. Mesocarp pigments influence grain color during milling.

Testa:

The highly pigmented layer just beneath the pericarp is known as the testa or sub-coat. It may or may not be present in a genotype. Testas vary in thickness and between genotypes. It is generally thickest near the crown and thinnest near the embryo of the seed. Testa pigmentation which influences seed color, is associated with polyphenols or tannins (Glueck and Rooney, 1980). Seeds having high tannins withstand better weathering and preharvest sprouting than seeds low in tannins; they also minimize the incidence of grain mold and bird attacks, and reduce dry matter digestibility by way of binding proteins and digestive enzymes.

Endosperm:

The endosperm consists of an aleurone layer, the peripheral corneous endosperm and the central floury portion. The aleurone layer is located beneath the pericarp, which consists of a single layer of narrow rectangular cells. The cells of aleurone layer under high magnification shows spherical bodies which contain large amounts of proteins, oils, minerals, water soluble vitamins and autolytic enzymes (Glueck and Rooney, 1980). They do not contain starch grains and play a great role in autolysis, as well as in the mobilization of food reserves during germination.

The location of the peripheral corneous portion of the endosperm is not well defined. It contains small compact starch grains embedded in a thick proteinaceous layer of 2 to 6 endosperm cells. It possesses free protein bodies, as well as matrix proteins. The matrix proteins are either glutenins, alkali soluble proteins, or prolamins. Their size and number decreases towards the center of the seed. The corneous portion of the endosperm possesses a continuous interface between starch and protein. The bond between the starch and protein is quite strong and allows starch granules to break from the matrix.

Just beneath the corneous portion of the endosperm are located several layers of large elongated and vacuolated cells forming the floury endosperm portion. Numerous air spaces exist between the starch granules and protein. The starch granules are spherical and are not held together by a protein matrix. The protein bodies and matrix are present in the floury endosperm. The matrix proteins form a thin, discontinuous sheet over the starch granules. The floury endosperm is very soft and susceptible to enzymic attack (Glueck and Rooney, 1980).

Embryo:

The embryo contributes approximately 10 % of the total dry weight of the seed. The scutellum, consisting of vacuolated parenchyma cells, has a well developed vascular system, and helps in the translocation of nutrients from the endosperm into the developing roots and leaf tissues of the embryonic axis during germination.

Hilum:

The hilum helps in the translocation of nutrients from the vegetative plant parts into the ovule during caryopsis development. This way also become the pathway for microorganisms into the seed. Translocation of the nutrients into developing endosperm takes place through specialized transfer cells in the scutellum (Giles *et al.*, 1975, and Gunning and Pate, 1969). A longitudinal section through the black layer zone reveals a layer of elongated vacuolated cells which shuts off the vascular connection of the seed from the rachis.

Relationship of seed maturity with nutritional composition

The developmental stages of starch and protein bodies in seeds were studied with a scanning electron microscope by Subramaniam *et al.* (1980) (Tables 2.2, 2.3).

Table 2.2 Composition of sorghum grain components at different stages of grain development (dry weight basis; Subramaniam *et al.*, 1981).

	Soft dough	Hard dough	Mature
Dry matter	59.69	75.59	89.22
Ether extract	2.86	3.33	2.86
Crude fiber	2.79	1.89	1.76
Crude protein	11.71	11.94	11.96
Total ash	1.79	1.40	1.42
Nitrogen free extract	81.03	81.50	82.00
Starch	67.33	69.94	71.34

The aleurone cells at soft dough and hard dough stages are distinctly visible. The peripheral endosperm at the soft dough stage show abundant protein bodies, and a starch grain size between 11 and 12 μm at maturity. The matured starch granules are tightly held in the peripheral endosperm and are affected by genetic and environmental factors (Sanders, 1955; Maxson *et al.*, 1971). The grains and protein bodies increase in thickness and size with time. The soft endosperm of the immature seed has large intercellular spaces. Sparse small and spherical protein bodies are also present in endosperm cells at soft dough stage with a diameter between 9 and 10 μm . At maturity the starch grains are loosely packed and have a diameter between 15 and 19 μm . They decline in number with maturity and are converted into the hard endosperm. The size of the protein bodies ranges from 0.75 and 1.00 μm , and these are embedded in the endosperm matrix. The starch granules at the middough stage are polygonal or globular in shape. They change into the polyhedral type progressively as the seed matures. At hard dough stage, the endosperm is not tightly packed and, in some cases, it is very loose. During the natural process of drying, the matrix protein loose water and shrink. The peripheral endosperm beam becomes hard and assumes a translucent appearance during drying. The intercellular spaces are filled with protein bodies and thick

matrix proteins at physiological maturity.

Table 2.3 Amino acid composition of sorghum grain (Subramanian *et al.*, 1981).

Amino acid	CONCENTRATION IN PROTEIN		
	Soft dough	Hard dough	Mature
Lysine	1.98	1.79	1.90
Histidine	1.95	2.02	1.96
Arginine	3.00	3.06	3.17
Aspartic acid	7.76	7.49	7.42
Threonine	3.10	3.12	3.13
Serine	4.94	4.81	5.09
Glutamic acid	22.79	22.94	22.50
Proline	8.89	8.81	8.42
Glycine	3.38	3.51	3.63
Alanine	9.77	10.03	9.57
Cystine	0.25	0.54	0.45
Valine	3.53	3.52	3.72
Methionine	1.64	1.63	1.60
Isoleucine	2.62	2.63	2.69
Leucine	13.13	13.21	13.14
Tyrosine	3.46	3.61	3.77
Phenylalanine	4.77	4.88	4.90

Crude protein, crude fibre and ash content decrease with maturity of seed, while the nitrogen free extract and starch content increase. The number and size of protein bodies increase progressively as maturity advances. The glutamic acid and leucine contents increase slightly with maturity while an inverse relationship is found for lysine and the total protein content (Table 2.2).

Grain dry weight accumulation and contents of soluble starch, protein, fat and ash were investigated by Subramanian *et al.*, (1983) in developing grains of sorghum cultivars. High lysine Ethiopian lines showed relatively low starch and high protein content at various stages of maturation, which suggests a possible mechanism of protein accumulation. Fat content showed a tendency to increase up to 28 days after flowering (Subramanian *et al.*, 1983).

PHYSICAL AND PHYSIOLOGICAL CHARACTERISTICS

A considerable diversity of physical and physiological characteristics exist in sorghum, and the general trends are briefly discussed here (Table 2.4).

Seed hardness:

Seed of different cultivars vary from very hard to soft; some are hard to break

and some are easily breakable. Seed hardness can be measured with the help of grain hardness tester. It measures the weight in kg required to break the seed. Grain hardness may be closely associated with the quality of the seed, as well as the weathering quality.

Table 2.4 Different seed characteristics (40 sorghum genotypes).

	Minimum	Maximum
Seed weight (30 seeds, g)	1.17	1.70
Seed length (mm)	3.22	5.85
Seed breadth (mm)	2.15	5.00
Seed thickness (mm)	1.14	3.45
Corneous rating	1.00	5.00
Grain hardness (kg)	1.66	11.19
Density	0.85	1.52
Total water uptake (6 hrs)	0.05	0.48
Water uptake % (6 hrs)	13.70	47.10
Percentage germination	36.70	63.30
First leaf area (cm)	0.30	2.42
Seedling dry wt (30 seeds, g)	0.05	0.37

Density:

Density is the mass per unit volume of a substance, and is measured by the displacement of distilled water:

$$\text{Density} = (\text{weight of the seeds in grams}) / (\text{volume of the seed})$$

In the case of sorghum the density differs widely in different genotypes within a range of 0.85 to 1.52.

Water uptake:

Water uptake is the capacity of the seed to absorb water. It is expressed in percentage over the original seed weight after a definite period of immersion. This may be related to the cooking quality of the seed. Studies in different cultivars indicate that water uptake ranges from 13 to 47% (based on dry seed weight and observations six hours after imbibition).

Variability for different morphological and physiological characteristics

The different morphophysiological characteristics of seed size in sorghum belonging to different taxonomic groups were studied by the author at ICRISAT in India. The genotypes included in this study showed significant differences for all the characteristics studied indicating that there is enough variability to select for these traits (Table 2.4).

Viability for seed wetting and drying

Sorghum has the capacity to survive germination and emergence, even if the emerged plumule and radicle dry up, one the conditions become favorable again.

Genotypic differences were noticed in the stand establishment when subjected to soaking and drying treatments. This is a useful trait for areas where seeds are dry and the rainfall is sufficient to initiate germination, but inadequate to ensure emergence. The testing technique involves cycles of wetting and drying for different time intervals followed by standard planting and germination in the field.

Soaking seed in water and drying to original seed weight induces faster emergence, more vigorous growth and higher yields. Such treated seeds remain viable if the radicle has not emerged, and may be stored for dry planting (Heydecker, Coolbear, 1977; Hegarty, 1977). Scientists at the Dryland Farming Research Scheme in Botswana noticed significantly greater differences for emergence of seeds soaked for 24 hours and dried than in the control seed (unsoaked), and results were consistent.

Considerable differences exist among different species in their germination at a given level of soil moisture (Bhan, 1970). Manohar and Heydecker (1964) found that seeds of certain species may germinate even when the soil moisture level is at permanent wilting, therefore, genotypes which have the capacity to germinate with lower degree of hydration may stand better chances of germination in semi-arid rainfall areas.

Seeds of cereal crops like *Pennisetum typhoides* and *Sorghum vulgare* are able to germinate at lower levels of water potential than the seeds of legume crops. In the arid and semiarid zones, where rains are uncertain and erratic, showers are often sufficient for germination but not sufficient for emergence. High temperatures, soil moisture gets depleted and germinating seedlings dry in the soil (Ramírez and Bejarano, 1973). Watt (1973) reported that some species can germinate in the soil moisture with tensions of -5 to -10 bar, but the embryo does not develop. Sorghum seed germinated with the availability of sufficient soil moisture, but this may not be adequate for emergence. Hegarty (1977) reported that cucurbits and carrot can germinate in dry soil, can survive dehydration and rejuvenate under favorable conditions. Increasing water content in the seed before sowing favors emergence (Lyles and Fanning, 1964); soaking and drying treatment affects the viability of sorghum seed (Jowett, 1965).

The author developed techniques at ICRISAT in India and at the University of Nuevo León in México, for the evaluation of sorghum cultivars against drought stress factor. In one study at ICRISAT (Maiti, 1980, unpublished), sorghum genotypes belonging to different taxonomic groups were tested for germination in Petri dishes in two replications for 20 hours. Subsequently, the germinated seeds were dried at 40°C in the incubator for two days and then kept at room temperature for ten days. These genotypes were studied for their emergence capability by sowing them in wooden flats. Significant genotypic differences were noticed in emergence; this stress factor can be attacked with stress resistant sorghum genotypes.

Effect of soaking treatment on seed viability and seedling vigor

In another study, seeds of 34 sorghum genotypes were soaked in water in Petri dishes for varying periods ranging from 4 to 28 hours (at 4 hour intervals) and

transferred to an incubator for drying at 35°C for 36 hours. Thereafter, germination tests were carried out to establish the differences among these treatments. Soaking pretreatment up to 20 hours did not have much effect on seed viability. There was a marked decrease in seed viability with increase in soaking beyond 20 hours. It was interesting to note that all the cultivars germinated within 16 hours. The elongated radicles had produced minute hairs by 20 hours of pretreatment, but the seed was viable even after the radicles and plumules were fully dried. After 28 hours of pretreatment, more than 10% of the seed germinated even after the long radicles and plumules were dried (Fig. 2.14).

The effect of the soaking treatments on seedling vigor was studied at ICRISAT. In this study, the seedling weight was measured after a five day growth in Petri dish culture and a marked decrease was noticed in seedling dry weight (Fig. 2.15). In another study, a direct correspondence was observed between soaking time and increase in mold infestation (Fig. 2.16).

In México, the technique was further modified (Maiti *et al.*, 1983a). Seeds were soaked in water for different periods (4, 8, 12, 16 and 20 hours) in Petri dishes followed by drying in an incubator at 35°C for seven days. Thereafter, the treated seeds were sown in soil and the percentage of emergence and dry weight of seedlings at 15 days was measured. Significant variance was observed between genotypes and treatments. Increase of emergence percentage and seedling dry weight was noticed in the four and eight hours soaking treatments. Henceforth, a gradual decline was observed as the hours of presoaking increased and the minimum was reached between 16 and 20 hrs. At ICRISAT the author found that some genotypes did not lose their viability even after 36 hours of soaking pretreat-

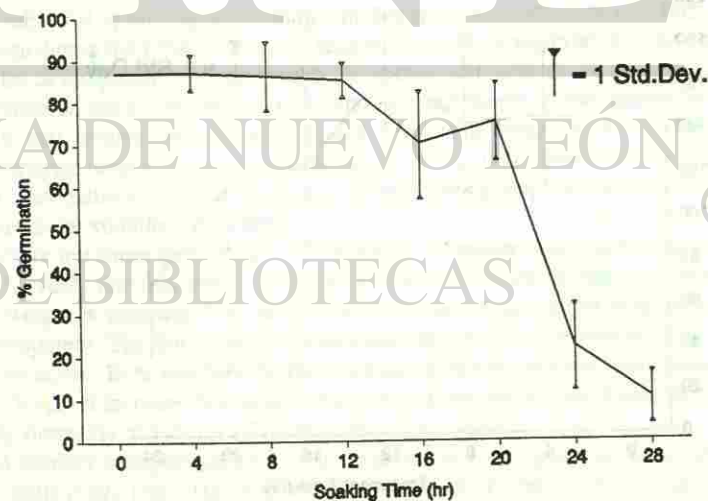


Figure 2.14 Germination % after different soaking times and drying for 24 hr at 40°C.

ment followed by drying for 10 days at 35°C in an incubator (Maiti, unpublished). The use of these lines needs to be tested in dry sowing conditions, and sorghum germplasm may be screened for this trait.

In Mexico, Moreno-Limón (1988) demonstrated that some genotypes did lose their viability even after 40 hrs of presoaking and drying at 35°C for 15 days. Also, genotype resistance seems to be linked to a specific protein which is absent in susceptible strains (Maiti, 1989, unpublished). Genotypes selected for this resistance traits could be recommended for dry sowing under rainfed situations in semiarid regions such as in temporal agriculture in Mexico.

Associations among different morphophysiological characteristics

The relationships among different seed characteristics may be used to identify certain useful traits of seedling growth. Seed size (weight) shows significant positive association with seed dimensions ($r = 0.8$), total water uptake ($r = 0.8$), and seedling dry weight ($r = 0.8$). The total water uptake at six hours is significant and is positively correlated with seed dimensions and seedling dry weight ($r = 0.8$), but water uptake (%) is negatively associated with seed size and dimensions. Seed dimensions (thickness, length and breadth) and scutellar length are well associated. Grain hardness is significant and positively correlated with seed length, breadth and length of the scutellum, and also with corneousness. First leaf area is positively associated with the seedling dry weight, which is well associated with seed size.

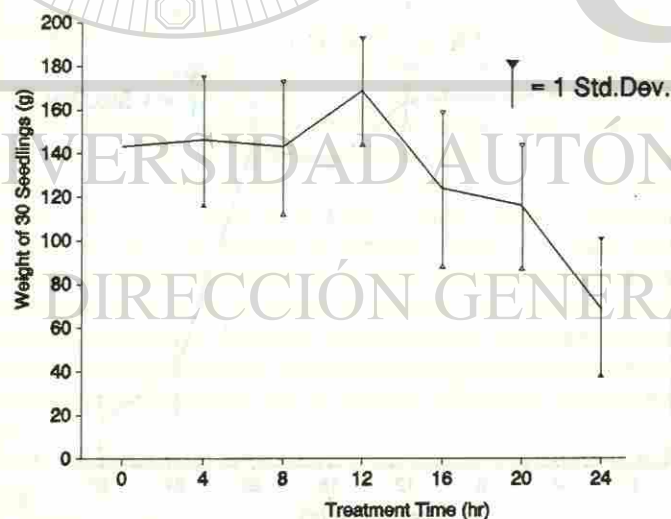


Figure 2.15 Effect of the duration of the soaking treatment on the vigor of the seedlings.

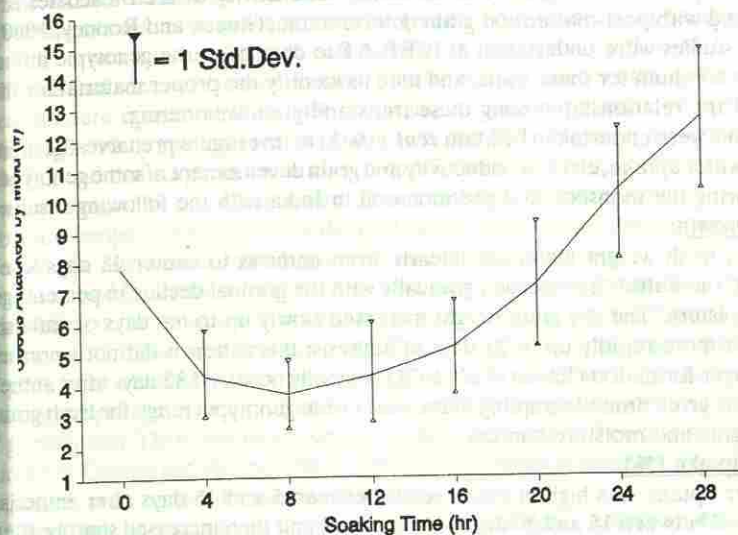


Figure 2.16 Effect of the soaking treatment on mold infestation of the seedlings.

GERMINABILITY AND SOME ASPECTS OF PRE-HARVEST AND POST-HARVEST

Preharvest sprouting is the major problem in early sorghum cultivars which mature during the peak of the rainy season. This affects seed viability and enhances the development of grain molds. Enzymes activated or synthesized during germination initiate the hydrolysis of endospermic starch, cause chalkiness of the grain that reduce the test weight, and provide a congenial environment for saprophytic fungi (Castor and Frederiksen, 1977, 1980). Seed dormancy during and after maturity helps to reduce grain weathering, improves seed quality and protects the viability of the seed.

There are three mechanisms for retaining dormancy in sorghum (Clark *et al.*, 1967, 1968). The first one is to maintain moisture at 28% or less until maximum dry weight is attained. The second one is to select genotypes with rapid seed development. The third one functions when the previous two mechanisms are no longer active. In brown hybrids, the presence of brown pericarp and brown teeth also helps to increase dormancy. Dormancy is greater in late flowering than in early flowering genotypes (Grittons and Atkins, 1963).

A number of reports are available on preharvest seed germination in sorghum (Kersting *et al.*, 1961; Harris *et al.*, 1962; Clark *et al.*, 1967). The tannin content of the testa is associated with reduced preharvest germination (Harris and Burns, 1970) and reduced preharvest grain molding (Harris and Burns, 1973). The rate

of water uptake by the grain and electrical conductivity of seed leachates associated with post-maturation grain deterioration (Glueck and Rooney, 1967). Similar studies were undertaken at ICRISAT to determine the genotypic differences in sorghum for these traits, and then to identify the proper material for study of the relationship among these traits and grain weathering.

Studies were undertaken by Maiti *et al.* (1985) to investigate preharvest grain quality, water uptake, electroconductivity and grain development of some genotypes both during the monsoon and postmonsoon in India with the following results:

Grain growth:

Grain fresh weight increased linearly from anthesis to center 25 days after anthesis; thereafter, it decreased gradually with the gradual decline in percent grain moisture. The dry grain weight increased slowly up to ten days of anthesis and then more rapidly up to 25 days of anthesis; thereafter, it did not increase. Black layer formation (Eastin *et al.*, 1973) normally occurred 32 days after anthesis. At any given time of sampling, there was a wide genotypic range for fresh grain dry weights and moisture content.

Water uptake (%):

Water uptake was high in young seeds between 5 and 15 days after anthesis; it dropped between 15 and 30 days after anthesis and then increased sharply at physiological maturity. The genotypic variability was small during the period of grain development. Mean rates were low, but increased significantly by the 40th day; this characteristic may be of significance for resistance to weathering and prevention of germination on the panicle when they exposed to rains (Castor and Frederiksen, 1977).

Electroconductivity:

The electroconductivity of the seed leachates did not change five days after anthesis near the black layer stage. Thereafter, it increased significantly together with water uptake. Genotypic variability was considerably greater for conductivity than for water uptake during the whole sampling period.

Germination:

Most genotypes began germination between 20 and 30 days after anthesis; however, actual percentage of seeds germinated during this period varied considerably among different genotypes. After 30 days of anthesis, when all experimental lines had initiated germination, germination ranged from 3 to 100%. After 40 days of anthesis the minimum germination was 76 %, indicating that at the time of physiological maturity (about 10% moisture) no significant dormancy existed in any of the lines. A number of genotypes had less than 50% germination at 35 days after anthesis (IS 6127, IS 6205, IS 6204, IS 9374, IS 3921 and IS 165). The advantage of grain trait under field conditions during the rainy season is not yet fully established.

Germination initiated among the lines tested in the post-monsoon was similar to that during the rains, however, germination began earlier, as 5% of the lines initiated germination at 10 days after anthesis, and this went up to 92% at 25 days after anthesis. At physiological maturity, all the lines had initiated germination but nearly 50% of the lines showed less than 50% germination. Some lines showed less than 10% germination (IS 2074, IS 4310, IS 6131, IS 9333, IS 15021, IS 15709, IS 16201 and IS 16657). In all these studies, genotype and genotype X time of sampling were significantly different in all the parameters studied.

The moisture content of the seed at the time of sowing is considered to be a factor that can influence germination (Phillips and Youngman, 1971). Seeds must contain a certain moisture content before they can germinate. Clark *et al.* (1968) indicated that seeds of the non-dormant 'Shallu' cultivar will germinate when the seed moisture content is 32 to 34%. Emerging radicles were visible on seeds of hybrid RS 610 by the time the seed moisture was 25%. Nutile and Woodstock (1967) found that sorghum seeds sown with 8% moisture emerged less than seeds sown with either 11 or 14% moisture. Low initial seed moisture content and low substrate temperature resulted in delayed radicle protrusion from the pericarp, as well as a decrease in seed respiration rate during imbibition.

Castor and Frederiksen (1977, 1980) have shown that the germinability during grain-filling in the rainy season promotes the growth of saprophytic fungi and grain deterioration. In the present study, a significant range of variance in germinability of grain were observed before physiological maturity of the seed. At the harvest maturity stage (about 40 days after flowering), most of the genotypes were capable of germination. These results are similar to those reported by Brown *et al.* (1948), who noted by Gritton and Atkins (1963). Only 5/147 varieties of sorghum were found to possess even partial dormancy at harvest.

There was an increase in electroconductivity and water uptake in the later stages of grain development which may be associated with an increase in permeability of the membrane at this stage, either naturally or due to weathering. Entry of water into the seed and leaching of materials out of the seed at harvest maturity were not correlated. Conductivity was less in seed with a corneous endosperm, though the water uptake appeared to be independent of the corneous rating of the endosperm; conductivity and water uptake appear to be governed by different factors.

Rate of water uptake:

The rate of water uptake was correlated only to seed size, which may reflect the greater surface or volume ratio in smaller seeds. A combined analysis of the common variables gave evidence of a seasonal difference in the dormancy of certain entries. Sampling procedures for germinability, water uptake, etc., should consider the effects of the environment, the stage of development and the maturity of the seed. Some genotypes which showed some level of dormancy of physiological maturity (30-35 days after anthesis) were identified in both monsoon and post-monsoon seasons, i.e. IS 83, IS 188, IS 219, IS 1235, IS 1352, IS 2468, IS 6117 and IS 6204. It is not known whether this delayed germinability has a measurable effect in grain weathering and the sprouting of the seeds during the rainy season. As there was no dormancy following physiological maturity, these lines will be affected only by rains occurring after maturity. Therefore, instead of looking into these lines in more detail, a large number of germplasm lines should be screened for entries which are dormant at late stages of maturity (about 40 days after anthesis) and which would be more useful to breed for weathering resistance. Therefore, concerted research efforts should be directed towards developing weather-resistant lines.

In 1990, Maiti and Banerjee (unpublished) showed that grain mold infestation during grain development severely affected the emergence and seedling vigor of

sorghum genotypes. Large genotypic variability existed for seedling emergence and seedling vigor of the sorghum genotypes infested with grain mold. Therefore, concerted efforts should be directed to eliminate the deteriorating effect of mold on sorghum grain quality during the growing period of the crop.

GENERAL COMMENTS

The morphophysiological characteristics of different sorghum genotypes show considerable variations in seed size, shape and dimensions, surface orientation, seed structure, distribution pattern of corneous and floury endosperm, hardness, water uptake, seed viability, first leaf area and seedling dry weight, and that all the variations in these characters are statistically significant. An interesting fact is that most genotypes do not lose their viability even after presoaking for 40 hours when the radicles and plumules are advanced in growth and then transferred to the incubator for 15 days at 35°C (Moreno-Limón, 1988). Lines selected for resistance to presoaking and drying could be useful in an area where dry farming is practiced. Different seed morphological traits were found to show relationships among themselves. They have shown relationships with some of the physiological functions, for example, seed size is related to grain hardness, total water uptake, first leaf area and seedling dry weight. Seed size is negatively correlated to percentage water uptake. Grain hardness is positively associated with the corneous endosperm content; the first leaf is positively correlated to seedling dry weight. These characteristics could be used as selection criteria for better seedling growth.

Sorghum grain attains germinability even before the attainment of physiological maturity. Some start germination at an early stage of grain development, others germinate at a later stage. In order to avoid grain weathering, we should look for genotypes that show no germinability at major stages of grain maturity. A number of lines have been selected at ICRISAT which show dormancy up to a late stage of physiological maturity. Proper care needs to be taken not to use seeds affected with grain mold causing poor seedling vigor.



GERMINATION AND SEEDLING ESTABLISHMENT

INTRODUCTION

Germination, emergence and establishment of seedlings are vital to plant development. Many morphogenetic changes take place simultaneously before the establishment of a seedling. These processes involve complex serial, structural and metabolic transitions in possibly adverse situations under erratic environmental conditions. These processes are interrelated, and knowledge of the interactions among them help in the understanding of the plant's condition at each stage of development. The normal process of seedling development is largely controlled by environmental factors and influences the development of the adult plant. Seedling establishment is one of the major obstacles of crop production in the semi-arid tropics (SAT) (Maiti, 1983, 1986). Despite adequate fertilizer use and irrigation, the yields are often low in some crops due to poor plant stands, which is a consequence of poor seedling emergence and establishment. Adverse conditions encountered in the SAT countries, like varying planting depths, limited moisture, high soil temperature, soil crushing, etc., affect seedling emergence. Therefore, improvement of seedling vigor and testing breeder's lines for crop establishment traits should be the major considerations in a breeding program. Investigations in this direction have clearly established that which is discussed herein.

Biological and environmental factors associated with screening for improved germination and establishment in different crop species have been reported by different workers (Kneebone, 1970; Wright, 1971; McKell, 1972). There has been a good amount of work relating seed characteristics with seedling vigor in different crops (Kneebone and Cremer, 1955; Isley, 1958; Kalton *et al.*, 1959; Christie and Kalton, 1960; Tossell 1960; Dhindsa and Slinkard, 1963; Lawrence, 1963; Maiti, 1981). Kneebone (1970) considered the seed size as the most promising selection criterion available to the breeder to improve seedling vigor. Seed size was related with early growth and grain yield in barley, and high protein content and seed size were related to good seedling vigor in wheat (Kaufmann and McFaden, 1963; Kaufmann and Guitard, 1967; Dasgupta and Austerson, 1973; Sterling *et al.*, 1977; Ries and Austerson, 1973). Seeds with high protein content in wheat produced more vigorous seedlings than those with low protein (Welch, 1977; Bullisani and Werner, 1980).

Ching (1973) reported that seed weight, adenosine triphosphate (ATP) and adenosine diphosphate (ADP) contents of the hydrated embryo were good vigor

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Biological and environmental factors associated with screening for improved germination and establishment in different crop species have been reported by different workers (Kneebone, 1970; Wright, 1971; McKell, 1972). There has been a good amount of work relating seed characteristics with seedling vigor in different crops (Kneebone and Cremer, 1955; Isley, 1958; Kalton *et al.*, 1959; Christie and Kalton, 1960; Tossell 1960; Dhindsa and Slinkard, 1963; Lawrence, 1963; Maiti, 1981). Kneebone (1970) considered the seed size as the most promising selection criterion available to the breeder to improve seedling vigor. Seed size was related with early growth and grain yield in barley, and high protein content and seed size were related to good seedling vigor in wheat (Kaufmann and McFaden, 1963; Kaufmann and Guitard, 1967; Dasgupta and Austerson, 1973; Sterling *et al.*, 1977; Ries and Austerson, 1973). Seeds with high protein content in wheat produced more vigorous seedlings than those with low protein (Welch, 1977; Bullisani and Werner, 1980).

Ching (1973) reported that seed weight, adenosine triphosphate (ATP) and adenosine diphosphate (ADP) contents of the hydrated embryo were good vigor

predictors for high emergence rates in barley cultivars. Lawrence (1963) concluded that seed weight in rye grass was controlled to a large extent by the maternal parent, and that additive gene effects were responsible for explaining the genetic variation in the number of days to emergence. He found also a slight association between seedling growth and adult plant characteristics in Russian wild rye. This indicated that selection in the seedling stage could also have some bearing in breeding for higher yields. Lawrence (1963) suggested that breeding for improved seedling vigor in Russian wild ryegrass would be accomplished by selecting for large seed lines and then subjecting them to deep seedling in greenhouse or in the field. No such studies have been made on sorghum or millet.

Laboratory seed germination following ammonium chloride pretreatment is reported to be a useful technique for assessing seedling emergence in sorghum (Abdullahi and Vanderlip, 1972; Vanderlip *et al.*, 1973, and Yayock *et al.*, 1974). Vanderlip (1974) thought that the field establishment of pretreated seeds should show maximum efficiency in quick germination and rapid emergence. Arkin (1976) built up a simulation model for sorghum emergence.

Genetic variations for salt tolerance has been documented in different plants and crops such as corn (Schubert and Lauchli, 1986; Hajibagheri *et al.*, 1986), wheat (Gorham *et al.*, 1986), barley (Hurkman and Tanaka, 1987; Ramagosa *et al.*, 1988), sorghum (Weimberg *et al.*, 1984; Grieve and Maas, 1984; Boursier *et al.*, 1985) and Johnson grass (Yang *et al.*, 1989).

Sodium chloride salinity inhibited sorghum seedling growth and small seeds were most sensitive to salinity (Amthor, 1983). Grain sorghum is moderately tolerant to salinity, indicating that the yield reduction was due primarily to low weight per head, and vegetative growth was affected less than grain yield by salinity increase. Sorghum grain was more tolerant at germination than at later stages of growth (Francois *et al.*, 1984). Responses of sorghum to different concentrations of sodium and potassium salts were reported by Weimberg *et al.* (1984) who indicated that concentrations of inorganic phosphate, glucose, fructose, amino acids and malic acid fluctuated in both roots and leaves, in association with saline stress.

The degree of salinity tolerance of a species may depend on several complex mechanisms operating at anatomical, morphological, physiological, biochemical or gene expression levels (Flowers *et al.* 1977; Storey and Wyn Jones, 1981; Gorham *et al.* 1985; Munns and Termaat, 1986; Sachs and Ho, 1986; Thiel *et al.* 1988). Leaf extension is one of the most susceptible processes in plants sensitive to salinity stress (Munns and Termaat, 1986 and Aspinall, 1986). Salinity affects photosynthesis through the reduction in photosynthetic surface in *Beta vulgaris* (Papp *et al.*, 1983). Salinity was related to increased respiration rates (Schwarz and Gale, 1981). This was also observed in *Phaseolus*, *Xanthium* and *Atriplex* but not in *Zea*. Others have shown that salinity limited the assimilation of CO₂ in two ways: 1) the response of stomata to plant salinization, and 2) the capacity of plants to fix CO₂ (Longstreth *et al.*, 1984; Seeman and Crichley, 1985; Ball and Farquhar, 1984). Mechanisms of salinity tolerance in plants were reviewed by Cheeseman (1988) involving cellular and organismal metabolism relating to control and

integration of sodium ion acquisition and allocation, and those in readjustment of other aspects of metabolism, especially the carbon source. Osmotic adjustment and ion regulation in plant cells subjected to salinity are the best known model of the different mechanisms of plants to achieve salt tolerance (Flowers *et al.*, 1977; Greenway and Munns, 1980; Munns and Termaat, 1986; Binzel *et al.*, 1988). Glenn (1987) studied the role of cation accumulation and water content on the osmotic adjustment of several salt-tolerant grasses, reporting accumulation of Na⁺ and lowering the water content as main strategy of osmotic adjustment.

CROP ESTABLISHMENT IN SORGHUM

Crop establishment in sorghum is affected by a number of factors related to the seed and its environment (Table 3.1). Two important aspects of crop establishment are (Fig. 3.1): 1- events and conditions existing in the seed zone below ground from sowing to seedling emergence; 2- problems and factors affecting the seedlings from emergence to the final establishment above ground.

Major limiting factors to crop establishment are: 1- emergence; 2- seedling vigor; 3- drought susceptibility of seedlings; 4- response to available nutrients; 5- susceptibility to salinity.

The various factors affecting crop establishment are examined here at two distinct stages of plant development: 1- germination to emergence; 2- emergence to panicle initiation.

Table 3.1 Factors affecting seedling emergence in sorghum.

A. SEED CHARACTERISTICS	B. ENVIRONMENTAL FACTORS
i) Seed management	i) Edaphic
a) seed storage	a) water
b) seed treatment	b) heat
ii) Physical characters of the seed	c) crusting and compaction
a) size	d) aeration
b) weight	e) soil reaction
c) moisture percentage	f) nutrients (pH and salt concentration)
d) density	
iii) Physiological characteristics of the seed	ii) Aerial
a) grain maturity	a) light
b) seed viability	b) heat
c) seed dormancy	c) humidity
C. MANAGEMENT	D. BIOLOGICAL
i) tillage	i) weed competition
ii) depth of sowing	ii) disease
	iii) pests.

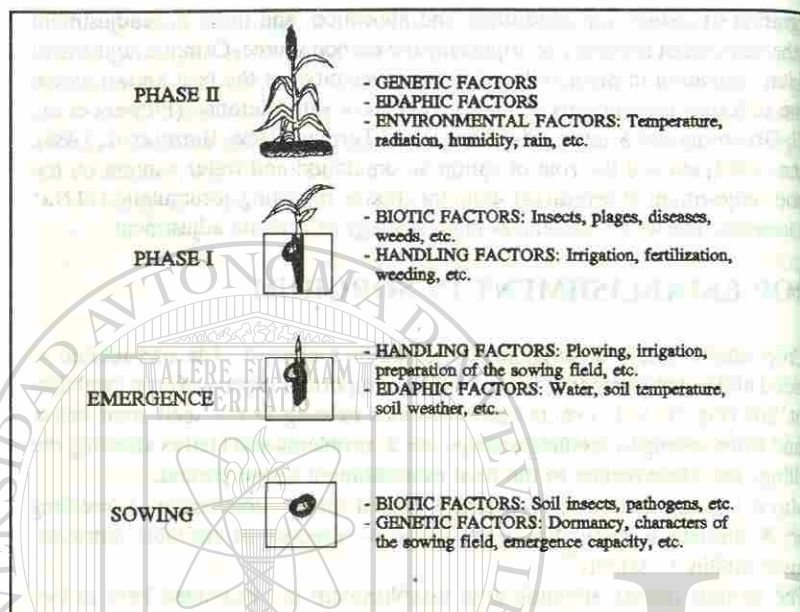


Figure 3.1 Factors that affect the establishment and productivity of crop.

Germination

Germination begins with the imbibition of water by the seed and ends with the emergence of radicle from the testa. Mayer (1977) wrote that the two important processes involved in germination are: the physical process of water uptake and the initiation of the complex biochemical steps following rehydration. The activity of the embryo is maintained by its constant supply of nutrients, which in turn maintains the heterotrophic system until the seedlings are able to photosynthesize and become autotrophic. Crop seed germination was reviewed by Gelmond *et al.* (1978).

Germination involves three important steps (Mayer, 1977): 1- utilization of low molecular weight compounds with ATP synthesis; 2- selective breakdown of storage compounds with the reorganization of the mitochondrial membranes; and 3- breakdown of storage materials with the synthesis of new mitochondria.

In sorghum, sucrose is synthesized in the scutellum and is the primary sugar translocated to the growing shoots and roots. Sugar accumulation in sink regions were well correlated with their disappearance in the source tissue (endosperm). Endosperm hydrolysis does not occur readily during the early growth phases, and by the second day, the hydrolytic breakdown of insoluble carbohydrates in the endosperm exceeded the rate of use by the seedling until the 8th day (Newton *et al.*, 1980). Carboxylase activity increase at early stages of germination is important for seedling development (Perl, 1978). Root emergence and enzymatic activities in sorghum are directly correlated with field performance, while proteinase activity

is inversely correlated with seed vigor (Perl and Luria, 1978). Optimum moisture content for germination in sorghum was reported between 35 and 40%, while germination occurred between 15-30°C with an optimum at 22°C. Active germination and growth were assessed in terms of soluble carbohydrate and total starch in the seedling. Glucose and maltose are the main simple sugars of the soluble carbohydrate (Aisien and Ghosh, 1978). Sucrose and raffinose levels in the scutellum of the intact sorghum embryo declined sharply through germination, but increased at radicle emergence as the hexose sugars from the endosperm passed into the scutellum; maltose, maltotriose and glucose were the main products of enzymatic hydrolysis of the endosperm carbohydrates during seedling development (Aisien, 1982).

Standard germination percentage, as a measure of quality, is inadequate for seed vigor evaluation under the usual range of less than optimum field condition. Therefore, other tests should be used to provide more realistic information (Caldwell, 1960; Moore, 1964). Not only the germination test, but other supplemental tests, viz. accelerated aging, cold test, seedling growth rate, etc., which would ensure better assessment of seed vigor (Ahmed, 1977). Prolonged aging over 72 hours under 45°C and 100% R.H. is detrimental to sorghum seed.

Dormancy

Research on seed dormancy in different crops is extensive, but few studies are available on sorghum. Grittons and Atkins (1963) reviewed dormancy in sorghum. Robbins and Porter (1946) reported that although some sorghum seeds germinate when their moisture content decreases to between 50-60%, freshly harvested sorghum seeds were often dormant. Casey (1947) noted unusually high percentages of dormant seed in germination tests, observing that some varieties were more likely than others to exhibit dormancy; varieties which shed their glumes at threshing were not as dormant as were varieties with attached glumes. Brown *et al.* (1948) studied the effect of storage on viability of oats, barley and sorghum seeds, finding that sorghum seed was not dormant after the grains had been stored for two months at 40°C. Seed dormancy was more common in sorghum than in barley or oats.

Goodsell (1957) found that scarification of the seed with a small file was effective to break dormancy in sorghum. Mechanical devices for scarification of larger seed lots were effective in breaking dormancy, but excessive damage could hamper germination. Soaking the seed in water at 70°C for four minutes was effective in overcoming dormancy. Another method to overcome dormancy was by prechilling the seeds at 5°C for six days and by continuing the test at 20-30°C until all viable seeds had germinated (Robbins and Porter, 1946). Stanway (1958) suggested that freshly harvested or immature sorghum seed need to be prechilled before germination tests. She subsequently found that lower germination was obtained for prechilled as compared to unchilled seed lots. The commonly used procedure for laboratory germination of sorghum seed requires the alternation of temperatures of 20°C for about 16 days, and 30°C for about 8 hours. Alternating temperatures resulted in better germination of Johnson grass, *Sorghum halepense* than did constant temperature (Stanway, 1959). Tester and McCormik (1954) showed that freshly harvested Johnson grass seed gave higher germination

percentage when prechilled at 10°C as opposed to 5°C.

Weir (1959) reported that ungerminated seeds of *S. halepense* did eventually germinate if caryopses were maintained under favorable conditions. Germination was more rapid at 30-45°C than at 20-35°C. Barton (1939) suggested that low temperature pretreatment known as 'stratification' is effective in inducing germination of seeds with a dormant embryo. Seed scarification was most effective in overcoming dormancy. Grittons and Atkins (1963), working on a range of genotypes, reported that they differed significantly in the level of dormancy which germinated at intervals of two weeks and a month after harvest. Seed dormancy was of little consequence three months after harvest. Kersting *et al.* (1961) showed that sorghum seeds are capable of germinating as early as 12 days after flowering and seeds harvested 12, 15 and 18 days after flowering were slower to emerge and had less seedling vigor than older seeds. Maiti (1983) reported that some sorghum genotypes have the capacity to germinate even 10 days after anthesis, and genotypes showed genetic variability in pre- and postharvest physiology. Clark *et al.* (1967) reported that three mechanisms were found to operate in dormancy. The first was associated with initial seed moisture which functioned until it was reduced to 28% or less. The second mechanism was associated with the active seed growth and functioned until the maximum dry weight of the seeds was attained. The third mechanism functioned after the two others were no longer active and occurred in seeds which had attained maximum dry weight and in which the moisture content was less than 28%. These mechanisms work only in intact seeds since excised embryo from 15-30 day old seeds were not dormant.

WATER UPTAKE AND MOVEMENT IN THE SORGHUM GRAIN

Grosh and Miller (1959) and Jowett (1965) studied water uptake and movement in wheat and sorghum seeds. Glueck and Rooney (1978) attempted to follow the pathways by which water enters the sorghum kernel, finding that in the floury endosperm of sorghum the primary entry pathway for water was the disruptive connective tissue between the pericarp and rachis (Fig. 3.2). It then entered the cross and tube cells of the pericarp and rapidly moved around the seed. Concurrently, water appeared to move through the hilum (black layer) into the germ layer. After 30 minutes, water moved into the endosperm at the point where the endosperm, germ and pericarp meet. Some water also entered the kernel in the cross and tube cells. After about an hour, they found that water movement was maximum near the upper area of the scutellum. They suggested that water move via the scutellum vascular system into the endosperm, and this was more pronounced after 90 minutes. Once the water was in the endosperm, it moved readily through the less organized central floury endosperm.

Water uptake from soil

Due to erratic rainfall and high evaporation rates in the SAT countries, the moisture in the soil is often inadequate for germination and seedling establishment. Under inadequate soil moisture, a smaller seed-water contact area reduces the rate of water uptake causing delayed germination (Hadas and Russo, 1974). Seeds of maize and cotton differed in total amount of water absorbed (Stiles, 1948, 1949, cited by Mayer, 1977; Gelmond *et al.* 1978). Stiles (1949, cited by Mayer, 1977) thought that the seeds in xeric habitats would have low water requirements for

germination. Water uptake by seeds from soil is influenced by the differential of water potential between the soil and seed. The movement of water takes place of course from regions of higher concentration to those of lower potential (Fig. 3.2). See also Osmond *et al.* (1980). Thus, the occurrence and rate of germination in the soil are considerably influenced by soil moisture (matrix) potential and hydraulic conductivity (Collins-George and Hector, 1966; Sedgley, 1963). As the growing embryo is spatially separated from the storage endosperm in a cereal grain, there is at first a rapid water uptake by the embryo followed by uptake by other tissues (Milthorpe and Moorby, 1974).

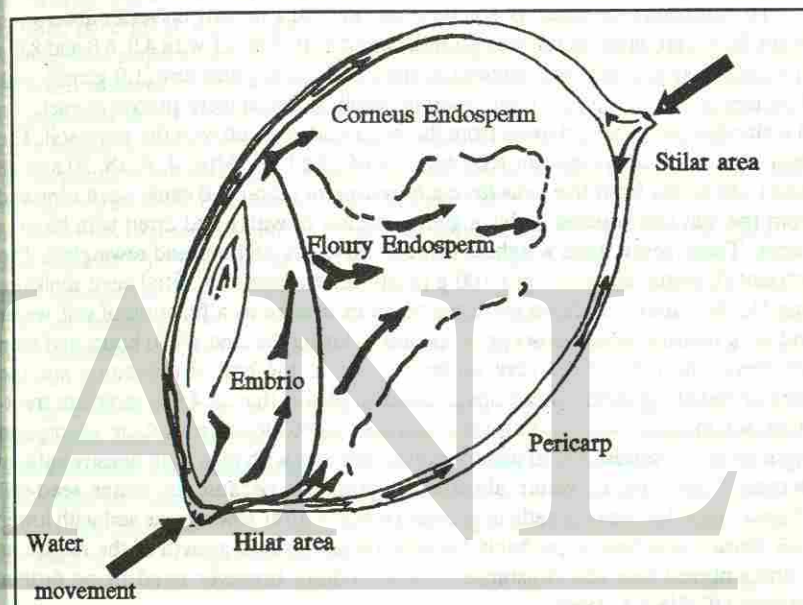


Figure 3.2 Water movement in sorghum grain (Glueck and Rooney, 1978).

Each seed has a specific hydration level below which germination will not occur. This hydration level is governed by the internal water potential for the seed. As the seed imbibes water during the early stage, its water potential increases, and during the later stages some internal metabolic changes occur (Hadas and Stibbe, 1973). When the seed attains the first critical hydration level, germination will occur. Mali *et al.* (1977) found that the critical seed hydration level in different sorghum varieties ranged from 21 to 34 % water; critical soil water potential ranged from -3 to -6 bar. Water absorption of 14 varieties of grain sorghum was studied at different moisture potentials (0.0, -0.3 and -4 bar). The seeds of all varieties did not require the same amount of water for germination. For a given time, the amount of water absorbed declined with a decrease in water potential. However, the total uptake increased with a corresponding lowering of the water

potential. The variation in absorption of water by the seeds might be attributed to the differences in the water requirement of embryo, the capacity and rate of water absorption by the endosperm, the hygroscopicity of the seed coats and the percentage of final germination. Mali *et al.* (1979) reported the seeds of CS3, SPV99, SPV302 and SPV370 probably exhibit adaptation to germination in arid lands which is indicated by their low optimal water requirement for germination. Soil moisture requirements for germination of sorghum, millet, tomato and Celosia were studied by Fawusi and Agboola (1980). They showed that both sorghum and millet performed well at low moisture regime which explains their ability to survive in dry ecological zones in excess of 50% field capacity.

To determine the effect of soil moisture and bulk density on water absorption by seeds, a 2 cm layer of soil was premoistened at ICRISAT with 4.9, 6.8 and 8.9% of water/100 g of soil and packed at high (1.8 g/cm³) and low (1.0 g/cm³) bulk densities in 8 cm diameter cans. Twenty sorghum seeds were placed in each can in a circular pattern 1 cm away from the walls and covered with the same soil. The cans were kept at a constant temperature of 23±1°C. After 4, 8, 18, 30 and 48 hours, the seeds from five cans for each treatment (total 150 cans) were removed from the soil and washed under a gentle stream of water and dried with blotting paper. These seeds were weighed, dried at 60°C for 48 hours and reweighed. The amount of water absorbed per 100 g of dry seed above the initial seed moisture was 11.3%. Table 3.2 shows the rates of water uptake as a function of soil moisture and bulk density. Water absorption declined during the first 18-30 hours and then reversed. The time of the reversal seemed to be the end of imbibition and the start of radicle growth. These observations indicate that at 4.9% moisture treatment, soil moisture was limiting whereas above 6.8% moisture level, the absorption capacity of the seeds limited water uptake. The soil with high bulk density initially increased the rate of water absorption, probably because of better seed-soil contact. With the start of radicle growth 18 hours after sowing, the soil with low bulk density was better, probably because of more rapid growth of the radicle as it encountered less soil resistance. These findings however need to be further verified (ICRISAT, 1980).

Table 3.2 Rates of water absorption by sorghum seeds as a function of soil water and bulk density.

Period after sowing (hr)	RATES OF WATER ABSORPTION (g/100 g per hour)			Bulk density (g/cm ³)	
	4.9	6.8	8.9	1.0	1.8
0-4	4.6	5.6	5.6	5.0	5.4
4-8	1.4	5.6	0.9	1.1	1.1
8-18	0.5	0.4	0.4	0.5	0.4
18-30	0.1	0.6	0.6	0.4	0.4
30-48	1.4	2.4	3.3	2.5	2.2

SEEDLING ESTABLISHMENT

Osmond *et al.* (1980) stated that the transition of germinating seeds to the established seedling in the soil is the most profound phase in the life cycle of an individual plant. A close coordination of absorption function for nutrients in the root and synthetic function of photosynthesis in the shoot is needed to maintain this vital process. It is a complex process which involves water relations, nutrition and morphological changes during establishment (Osmond *et al.*, 1980). Water relation of seedlings during establishment in any crop involves: 1- the structural changes occurring in the seed during the transition from nonvacuolated to vacuolated cells, and 2- the water environments of the seedlings due to the relocation of plant parts in the soil and the rapid changes in water content in the soil surface.

Nutrition requirement for initial establishment of the seedling is derived from the seed reserves of organic and inorganic materials until autotrophic response is generated in the seedling. In cereals, where seed reserves are predominantly carbohydrates, the metabolic transition of carbohydrates principally leads to the development of photosynthetic apparatus, whereas in the fatty seeds, it is a process of conversion of fat to carbohydrates (Mayer, 1977).

Efficiency of reserve mobilization can be calculated as follows (Khanna-Chopra and Sinha 1977): $\{[\text{Gain in seedling dry weight}]/[\text{Loss in kernel dry weight}]\}$. They have indicated from the study of some physiological and biochemical characteristics (*viz.* seedling growth, respiration rate, protein synthesis, etc.) that heterosis in germination and seedling growth could be because of complementary traits from the two parents.

Metabolic studies during seedling development of sorghum indicate that while the protein content declined in the endosperm, an increase was observed in the root and shoot of sorghum seedlings (Afria and Mukherjee, 1981). Asparagine and glutamine increased with seedling growth. Phosphoenolpyruvate and pyruvic acid constituted the main bulk of keto acid pool, while succinate, malate and citrate constituted that of organic acid pool.

In sorghum, the embryonic axis - the plumule - is capped by coleoptile and the radicle by the coleorhiza. Within the seed, about five leaf primordia are often revealed on microscopic examination. As the seeds swell with the absorption of water, the seed coat breaks. At first, the radicle is covered with coleorhiza and then the small coleoptile emerges through scutellum at the hilar region. The radicle grows downwards geotropically with the production of minute root hairs to give rise to the primary seminal root for establishment of the seedling. With the extension of the radicle, the coleorhiza is seen at the base of the radicle. The coleoptile grows upwards and emerges above the ground after 3 or 4 days, depending on factors like soil density, temperature, moisture, variety, etc. In colder climates (13 to 20°C), the emergence may be prolonged up to 10 days (House, 1980).

After emergence of the coleoptile, the first leaf breaks through the scutellum. The young plant begins to grow with emergence of embryonic leaves, and then with the addition of more leaves. The coleoptile remains as a sheath at the base of the seedling. The seed remains at the place of sowing, the mesocotyl elongates and the first node is found at the base of the coleoptile just below ground level.

Secondary roots begin to develop from this node when the plant is three to seven days old. Gradually, the seedlings are fully established with the development of the primary root and shoot system.

The response of plumule elongation in sorghum to moisture tension is more than that of the radicle and the lowest water potential at which seeds tested do not germinate largely depends on temperature (El-Sharkawi and Springuel, 1979). Again, matric water potential strongly controls emergence at all temperatures except at 28°C. In this study, plumule elongation was strongly suppressed with decreasing water potential at all temperatures, but more pronounced in the optimal temperature range (28-34°C). The effect of salinity stress on the emergence of the radicle and the plumule of sorghum was studied by El-Sharkawi and Springuel (1979a). Radicle emergence in sorghum decreased at -5 bar (Ψ) and plumule emergence at -7 bar (Ψ). The interaction of salinity with temperature on plumule emergence was significant. It was also reported that indole-acetic acid (IAA) promotes radicle emergence at low Ψ levels (-13 bar) in sorghum by increasing the permeability of cells to salts and promoting water uptake at relatively high levels of stress (El-Sharkawi and Springuel, 1979b). Seedling establishment is influenced by factors affecting seedling emergence, and those affecting establishment of seedling after emergence (Fig. 3.1).

Factors affecting seedling emergence

There are several factors affecting seedling emergence of sorghum (Table 3.1). Sorghum grain attains germinability long before the attainment of physiological maturity, although genotypic variability is found to exist (Gritton and Atkin, 1966; Clark *et al.*, 1967; Maiti, 1977). The germinability reached before physiological maturity of seeds may decline at latter stages of development (Srivastava and Pinnell, 1963). With the attainment of physiological maturity, the seed becomes dormant.

Standard laboratory germination is the measure of viability (Pinthus and Rosenblum, 1961; Vanderlip *et al.*, 1973). Retention of viability in storage shows an unusual pattern of decline with age, but seeds preserved in cold storage retain viability for a longer period.

Seeds of 3 sorghum varieties were soaked in water (40% water by volume) and the seeds started germinating, then they were removed and dried (to original level of moisture) under shade for 4 days; this seed-soaking treatment increased germination as compared to the controls (Parvatikar *et al.*, 1975).

Accelerated ageing of sorghum seeds was adopted by Gelmond *et al.* (1978) to allow them to imbibe moisture up to 17% at 20°C followed by additional storage in a closed container at 30°C. After various periods of ageing (0-48 days) seeds were tested for germinability at various time intervals. Percentage germination and field emergence percentage showed initial increment up to 16-20 hours and then declined sharply with time of ageing. Root emergence of sorghum seeds was found to be a function of time. All aged seeds maintained their original viability and none were killed.

Ageing brings about differences in seed viability (Gelmond *et al.*, 1978). There is a belief in practice that increasing seed water content before sowing improves emergence (Lyles and Fanning, 1964), but the potential advantage of water uptake

in corneous seeds which were more suitable for dry sowing than chalky seed, were highly affected by soaking and drying (Jowett, 1965). Raising seed water content in osmotic solutions which delay water uptake results in better subsequent performance (Heydecker, 1974).

Biochemical changes in sorghum seeds affected by accelerated ageing demonstrate that amylase, glutamic-pyruvic-transaminase, RNAase and glutamate decarboxylase follow the vigor profile with an increase after six days of ageing treatment followed by a decrease up to 48 days of ageing (Perl *et al.* 1978). There is an increase in proteolytic enzymes which may affect other enzyme concentration. It is concluded that the proteolytic enzymes may play an important role in sorghum seed deterioration during environmental ageing process. During ageing there were only small changes in the electrical conductivity of the seed leakage, and no significant differences in the rate of leakage of various compounds in the seeds as a result of internal concentration during imbibition rather than membrane deterioration. Therefore, the possible deterioration of the membrane during loss of vigor is overruled.

Sorghum seed can tolerate low water content, but rapid water uptake can do damage to the seedling (Nutile, 1964). Similarly, high temperature can damage seed in contrast to the deterioration of seed over long term storage (Ross and Webster, 1970). Maranville and Clegg (1976) have shown that high density improves emergence. Deterioration of seed quality not only reduces germination, but also may reduce vigor (Wilson and Eastin, 1982). In high altitudes, low temperature affects germination and emergence when there is substantial genetic variability (Miller, 1982). The optimum temperature for emergence was not examined by Evans and Stickler (1961), who found that shoot elongation was greater at 28°C than at 16°C. They report that genotypes varied in response to osmotic potential and temperature, and also according to the source of seed of each genotype. This was also affirmed by Wilson and Eastin (1982). Mali *et al.* (1979) have shown substantial differences between varieties in water uptake at the time of germination, and also differences within varieties in the rate of water uptake depending on water potentials of the soil. Stout *et al.* (1980) report delayed initiation, slow germination at low water availability in RS 610 where germination was reduced at -8 bars and fell to zero at -15 bars.

Evans and Stickler (1961) observed that between -8 and -14 bars, emergence rapidly declined from about 90% to zero. The time required for emergence ranged from 3 days to more than 10 days where temperature varied from 15.5°C to 22.2°C and moisture from field capacity to the wilting point.

Studies by Pathamanabhan and Sakharam Rao (1975) on salinity effects on seedling emergence indicate that seedling growth was much affected by salinity while the tolerant varieties exhibited better growth and tolerance. The reduction in dry matter was pronounced in all sorghum varieties. In another study, sorghum seeds were soaked in calcium chloride solution or distilled water for 24 hours. When the seeds were dried for four days in the open air until they regained their original weight. Seeds treated with calcium chloride gave higher yields than the control seeds (Naycem and Bapat 1976). Studies on germination of sorghum in 10 and 100 mM NaCl, NaHCO₃, and Na₂SO₄ indicate that there is a drop in the

level of reducing sugars at every stage of germination due to salt stress (Narabaunder *et al.*, 1979). Among the 3 salts used, Na_2SO_4 was more effective. Ogra Baijal (1978) reported that the varieties differed significantly in their ability to grow under high salt conditions and the inhibition of growth was more pronounced beyond 8 mhos/cm EC. Salinity affects nutrient uptake of sorghum in tolerant susceptible lines; tolerant varieties had higher accumulation of sodium compared to the susceptible ones (Pathmanabhan and Sakharan Rao, 1977).

Therefore, seedling emergence is the outcome of a complex interaction between the seed-bed environment and the seed. The seed passes from a dehydrated state to attain critical hydration through imbibition, resulting in cell elongation and meristematic activity. The growth of the coleoptile through a covering soil requires varying amount of force and finally emerges from the soil surface which leads to the shift from an energy consuming process to an energy producing process. A critical factor affecting seedling emergence is the physical condition of the seed-bed, its moisture supply, temperature and soil characteristics. The variability within a species for seed and seedling performance is of interest to crop scientists. Since the seed-bed environment is likely to be sub-optimal with receding moisture, the effects of moisture stress on the genotypes are related to a genotype performance over all seed-beds. At favorable temperatures, the rate of soil water uptake by imbibing seeds and the initiation of growth governs the germination process.

Depth of planting

Depth of sowing has profound effect on seedling emergence and the length of coleoptile and mesocotyl has been observed by Wanjari and Bhojar (1980), Maiti and Carrillo (1991). Deeper sowing is a normal practice in some African countries in zones of receding soil moisture. Irregular depth causes unevenness of seedling growth. The length of the coleoptile is considered an important attribute in determining the depth to which the seed could be sown in the soil (Banerjee, 1974). The length of the coleoptile is correlated to the culm length in wheat (Allan *et al.*, 1961). Attempts were made to select dwarf wheat with longer coleoptiles by hybridization (Chowdhury and Allan, 1963). Such studies need to be undertaken on sorghum. Maiti and Carrillo (1991) demonstrated that the sorghum genotypes showed great variability in elongation of mesocotyl under deeper planting depth and the emergence of seedlings is highly correlated to the mesocotyl elongation of the genotypes. They also showed that sorghum genotypes with longer mesocotyl showed higher seedling emergence, higher seedling vigor and seed viability, thus showing multiple stress resistance. An analysis of genetic parameters indicate that mesocotyl elongation is a reliable trait for its incorporation for stress resistance.

In one experiment by Maiti (1986) at ICRISAT, 10 genotypes were sown at depths of 20 mm, 30 mm, 40 mm and 50 mm, receiving a small shower upon sowing but none thereafter. Under the drying soil, seedling emerged from deeper depths. Seeds sown at 20 mm did not emerge, but with a first shower they started emerging; by this time, seedlings sown deeper were already established. This indicates that the seeds sown shallow did not lose viability, even when the germinating seedling were dried. The first shower was sufficient to complete the imbibition period, but it was not enough for the seedlings to emerge

above the surface layer. It was also observed that coleoptile and mesocotyl elongation play a major role in the ability to emerge when seeds of 200 genotypes were sown at deeper depth (20 cm). There was much variability in the length of mesocotyl. Many of them failed to emerge due to short mesocotyl, but those that did had mesocotyl length of 20 cm or more. The author assumes that the maximum depth from which a sorghum seedling can emerge is determined by the maximum elongation potential of mesocotyl in pushing the coleoptile to the surface of the soil. There was a great range of variability in the elongation of sorghum mesocotyl under greater depth of planting (Maiti, 1986).

Recent research at the University of Nuevo Leon, Mexico has shown that 100 sorghum genotypes have the capacity to emerge from 10-12 cm depth and genotypes showed significant differences for emergence from deeper depth and mesocotyl elongation showed positive correlation with the emergence from deeper planting (Maiti & Carrillo, 1991). This study supports the previous finding that mesocotyl elongation plays an important role in emergence when planting is deeper. There exists great genetic variability and genetic advance for mesocotyl elongation (Maiti & Carrillo, 1991).

Effect of seed size on seedling emergence

Gelmond *et al.* (1976) state that germinability of seeds under optimal conditions in the laboratory is not always a reliable criterion for their field emergence. He has observed that the weight of 1000 seeds with high germinability was higher than in those with lower germinability. Light colored seeds were superior to dark ones in their percentage and rate of emergence and in 1000 seed weight. Large sorghum seeds have an advantage over small seeds in the rate of germination and emergence. There was no difference between hand threshed and combine-threshed seeds in their emergence ability under optimal conditions.

Seeds grouped into 3 size classes were sown in wooden flats for seedling emergence studies. It was observed that seed size had no effect on seedling emergence in the same genotype. Genotypes differing in seed size were found to show significant variation in seedling emergence. Similarly, seeds taken from different locations (base, middle and top) in the panicle showed a significant variation in their capacity to emerge (Maiti, 1986).

The effect of seed size on seed viability, seedling vigor and seedling emergence has been reported by several workers (Abdullahi and Vanderlip, 1972; Suh *et al.*, 1974).

Soil temperature

High soil surface temperature is one of the causes for poor emergence in the SAT. Each plant has a minimum and maximum temperature at which no seeds germinate, and an optimum temperature at which germination will be highest. Soil temperature has a direct effect on both germination and subsequent plumule extension, thereby resulting in poor seedling emergence. In the SAT, air temperature often exceeds 40°C (Peacock, 1982). The minimum temperature for sorghum germination is reported to be between 7.2 - 10°C and 5.6°C for subsequent growth (Quinby *et al.* 1973). At the soil surface, temperatures > 60°C can be experienced by the emerging plumule (Peacock and Ntshole, 1976). Peacock

(1982) stated that optimum germination occurs when soil temperature is between 21 to 35°C and the lethal temperature for germination of sorghum ranges from 40 to 48°C.

Sorghum seeds were observed to germinate at 40°C but not at 47°C. Maiti (1982) reported that the minimum temperature may vary within species from 16.5°C. With an optimum temperature between 25 and 30°C, Singh and Dhaliwal (1972) obtained maximum germination at 25°C, but no germination between 5 and 10°C. The optimum temperature for radicle growth is nearly the same as for germination. Andrews *et al.* (1981) reported that 55% of the sorghum lines tested under simulated soil moisture conditions showed emergence at the seed zone temperature, while only 36% emerged at 48°C. Adams (1965), Bhat *et al.* (1971) and Unger (1978) found that surface residues influence soil temperature.

In a study at ICRISAT (1980), seedling emergence was noted with a set of 50 genotypes in a wide range of soil surface temperatures. Charcoal, light kaolin and heavy kaolin were used as surface covers to modify temperature. In the charcoal treatment, where temperature reached 65°C at 0.5 cm depth, there was no emergence, but most seeds germinated. The seedlings which failed to emerge did not show any sign of nutrient deficiency, and they appeared turgid. In the higher soil temperatures, the seedlings had emerged out of the coleoptile and unfolded slightly while still in the soil (ICRISAT, 1980). Details of the technique are described in Appendix-1. Wainwright *et al.* (1982) demonstrated that delayed and poor emergence were associated with high soil surface temperature. They observed that the plumule of the susceptible genotypes bent laterally after reaching high soil surface temperatures in charcoal while the coleoptile of the tolerant genotypes could emerge.

In another study, the author tested 50 sorghum lines at ICRISAT in India. Their emergence ability over a wide range of temperatures by planting on different dates between October 1980 and April 1981. Two different soil temperature profiles were obtained at each planting by using kaolin and charcoal as surface covers (Fig. 3.3). It was found that emergence was significantly affected by: 1- date of planting (environment), 2- surface treatment (kaolin and charcoal cover), 3- genotype, and significant genotype X treatment (2+3) interactions were observed. This indicated that genotypes behave differently in different treatments.

It was evident that with the increase in temperature from January to April at ICRISAT, there was decrease in emergence in the charcoal treatment. In the kaolin treatment, the emergence was relatively higher. During winter months, emergence took a longer time in kaolin than in charcoal due to the prevailing lower temperature in the former (ICRISAT, 1980). In these studies, emergence of seedlings showed significant negative association with temperature ($r^2 = 0.4$) at both soil surface and seed level (Maiti, 1986).

A set of 102 genotypes were again tested by the author with charcoal and kaolin 3 times - in November 1982, January and February 1983, and similar results were obtained. The date of planting (environment), surface temperature, genotype and their interactions had a significant effect on emergence. Both, low temperature in January planting and high temperature in May affected seedling emergence.

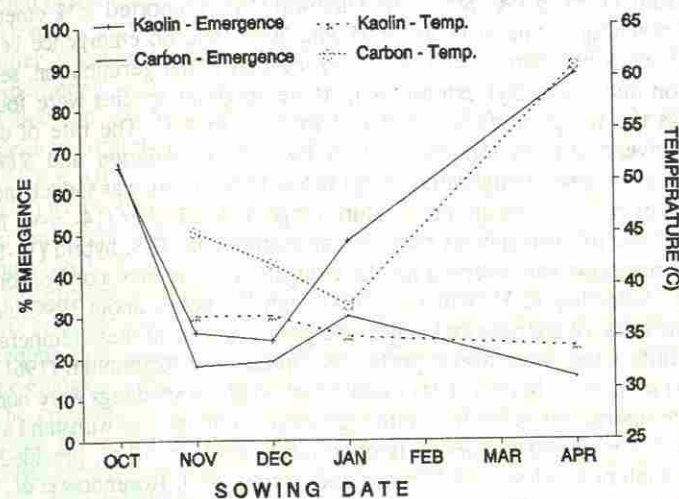


Figure 3.3 Effect of seasonal temperature on the emergence of seedlings in charcoal and kaolin.

Some genotypes were selected showing good emergence in low and high temperatures.

A technique was developed at ICRISAT in 1982 to study seedling emergence response to high soil temperature with no drought stress. Long clay pots (30 cm) filled with sieved alfisol (red soil) were kept in a water tank. Seeds were sown 50 mm deep in each pot. The soil was heated with a bank of infrared lamps fitted on a frame above the water tank. Temperature of 35 to 50°C at 20 mm depth could be maintained by varying the height of the lamps. Temperature was recorded at 6 hr intervals with a thermocouple, and the soil was heated until seedling emergence stopped 6 to 7 days after sowing. Sufficient moisture remained as water was supplied through capillary movement through the walls of the earthen pot. The test temperature was kept at 45°C. The maximum soil surface temperature in the field trials was reached on most days between 14:00 and 15:00 hrs. Using this technique, genotypic differences in emergence were most evident at 45°C. The effects of temperature, genotype and temperature X genotype interactions were highly significant. By simulating soil temperatures in the field, the technique can be used to screen genotypes to emerge through specified soil temperature under no drought situation (ICRISAT, 1982).

The effect of low temperature on germination and establishment of sorghum has been reported by several soil scientists and discussed further by Peacock (1982). Quinby *et al.* (1958, cited by Peacock, 1982) reported that the minimum temperature for germination is between 7.2°C and 10°C. Pinthus and Rosenblum (1961) quoted a range of 8-10°C. Both these groups indicated that a higher

temperature of 15.6°C was required for subsequent emergence. According to Thomas and Miller (1979), the minimum germination temperature varies with species from 4.6 to 16.5°C. Singh and Dhaliwal (1972) reported 55% emergence at 15°C reaching optimum between 25 and 30°C, and no emergence between 5 and -10°C. McWilliam *et al.* (1979) showed that initial germination, seed respiration and mesocotyl extensions in three sorghum species were found to decline as the temperature was reduced from 24 to 8°C. The rate of decline varied between species (*Sorghum leiocladum*; *S. verticilliflorum* and *S. bicolor*), especially in the lower temperature range below 12°C. There was sudden increase in Q_{10} values below a certain temperature range. It was higher (14-16°C) for more sensitive tropical species than for the commercial U.S. hybrid (11-12°C). A similar response was observed for the elongation of the mesocotyl of sorghum seedlings. According to McWilliam (1983), high Q_{10} below about 12°C indicate a high activation of energies and may cause poor response at these temperatures. Genetic differences were also reported by Pinthus and Rosenblum (1961), Stickler *et al.* (1962). Martin (1941) stated that sorghum seedlings were normally killed at temperatures below 0°C, although some seedlings may withstand a slight frost. Seed is reported to survive temperatures down to -12°C, provided soil moisture content is below 15% (Gritton and Atkins, 1963; Rosenhow *et al.*, 1962; Bass and Stanwood, 1978), but at higher moisture levels (30-35%) subsequent germination was markedly affected (Carlson and Atkins 1960; Rosenhow *et al.* 1962; Kantor and Webster, 1967).

Effect of soil crust on emergence

After sowing, soil crusting and compaction are important problems in semi-arid tropics (Miller and Gifford, 1980) where rain showers are often followed by sunny days. The surface crust creates impedence for the emergence of seedlings in different crops. Soil particles are rearranged to form a compact zone at the surface resulting in higher bulk density, less macroporosity and higher mechanical strength than the underlying soil (Lemos and Lutz, 1957; Tackett and Pearson, 1965). The sequence of events leading to crust is explained clearly by Richards (1953). Soil structure and texture greatly influences the strength of the crust (Mathers *et al.*, 1966).

Crusting has a direct effect on plant growth and an indirect effect on the desirable soil processes. The direct effect on plant growth includes mechanical obstruction to the emergence of germinating seedlings and damage to roots by the formation of warps and cracks in the drying crust. The indirect effect of crust on soil includes water percolation rate, increase in runoff and inhibition of microbial activity. Besides soil crust per se, bulk density of the soil was shown to affect seedling emergence in sorghum (Mali *et al.*, 1977). Some measures have been suggested to prevent crust formation. Of these, the use of mulches, chemicals and tillage are important (Mehta and Prihar, 1973; Chowdhury and Prihar, 1976; Khera *et al.*, 1976; Agrawal, 1980).

Different techniques were adopted to study the genotypic variability of sorghum for emergence ability through crust in the field and in brick flats. The results of a few experiments conducted at ICRISAT, Patancheru are described here (Agrawal *et al.*, 1986).

A technique for investigating emergence through simulated crust was developed and tested in the field. The technique involves preparing the land to a fine tilth, careful levelling and controlled perfo-spray irrigation. In one treatment, about six hours after irrigation a light roller (15 kg) was used to compress the upper layer. Two experiments were conducted by the author in summer 1980 with 100 lines, using rolled and non-rolled treatments. Significant rank correlations of seedling emergence in different genotypes between rolled and non-rolled treatments exist ($r = 0.74, P < 0.01$). Seedling vigor (seedling dry weight) was positively correlated ($P < 0.01$) to the ability to emerge through a crust (ICRISAT, 1980; Table 3.2). Further improvement of the technique is required as the coefficients of variation were high (28-33%).

An investigation was conducted by Inouye and Tanakamaru (1977) to study the effects of compaction of covering soil on the strength of plumule elongation and the seedling emergence of some cereals including sorghum. The strength of plumule-elongation under compacted soil was stronger than under non-compacted soil. The crosssection of the plumule was larger in the plumule grown under compacted soil cover, showing also higher bending strength. Crops with long mesocotyls exhibit high seedling emergence followed by crops with short mesocotyls or short coleoptiles.

The emergence of sorghum genotypes under crust conditions in the arid soils at Hissar, India was compared with that in the alfisols at Patancheru, ICRISAT (Tables 3.3 - 3.7). The main objective was to establish whether genetic variability existed and to identify genotypes which emerge well through soil crusts in both soil types (Agrawal *et al.*, 1986; for details of the technique, see Appendix 1). Significant treatment X genotype interaction was obtained, indicating that genotypes behaved differently; some lines showed better emergence in all crust situations. Crust strength in the alfisol field increased 4 to 6 kg/cm² during the period of seedling emergence, while in the brick containers it was only 2 kg/cm². The higher crust strength in alfisol could be associated with subsoil compaction in the field situation whereas in the brick container, the crust is thin (2 - 3 mm thick) and weak. As expected, there was gradual depletion of soil moisture with time, accompanied by a small increase in soil temperature. This brought about a marked

Table 3.3 Effect of crust on the emergence of seedlings (means of % emergence, significant $P < 0.01\%$).

	Exp. 1	Exp. 2	Exp. 3
Mean of treatments with crust	32.4	19.8	38.4
Mean of treatments without crust	52.4	42.0	54.6
LSD at 5% of genotypes	4.0	1.3	21.8
LSD at 5% of treatments	11.6	9.9	11.0

* Experiments: 1- 31 genotypes at Hissar, 2- 45 genotypes at Hissar, 3- 101 genotypes at Hissar. (LSD= least significant difference).

increase in crust strength in the field and in the brick containers, mean percentage emergence was higher in the field than in at the brick containers at ICRISAT, though the crust strength was higher in the field. This appeared to be due to emergence of seedlings through several cracks in the field, which did not occur in fine grained soils in the brick container.

Moisture content of the soil (Carnes, 1934; Sharma and Agrawal, 1978) as also structure and texture (Mathers *et al.*, 1966) are known to greatly influence the strength of the crust. The two test sites, Hissar and ICRISAT, have similar bulk density, but differ in other physical characteristics, consequently, the nature of the crust was different at the two locations. The aridosols at Hissar were low in organic matter and susceptible to surface crusting, and a thin layer of surface crust, 2 mm thick, was formed. The alfisols at ICRISAT, in addition to surface crusting, appeared to be prone to soil hardening while drying. The crust strength recorded by the penetrometer on the day of emergence was much higher in the alfisol where only surface crusting was involved. This explains the lower emergence in the crusted alfisols than in the aridosols, although the difference was very small (4%).

The percentage emergence on the first day showed a significant positive correlation with final percentage emergence in all experiments ($r = 0.59, 0.75$ and 0.5 in experiment nos. 1, 2 and 3 respectively; $P < 0.01$); similarly, the final percentage emergence showed a significant positive correlation with the emergence index ($r = 0.56, 0.56, 0.66$ in experiment nos. 1, 2 and 3 respectively; $P < 0.01$; Table 3.4). Also the rank correlation between emergence on the first and final day over all experiments was significant ($r = 0.70$; $P < 0.01$). Thus, as expected, the emergence on the first day may give an indication of the emergence on the final day. The lines that emerged earlier, often emerged better in the crusted soils. The genotypes which emerge faster are better suited for crusting soils. Therefore rapid emergence could be used as a preselection criterion for better genotypes under crust situations.

Since crust strength increased over time, the higher emergence in genotypes which emerged earlier may be ascribed to their emergence through a weaker crust. Thus the better emergence of these lines may be attributed to 'crust avoidance'. The faster rate of coleoptile growth and seed vigor could help these genotypes to emerge through crusts.

Analysis of data from all 3 experiments indicated that genotype, experiment

Table 3.4 Means and ranges of final seedling emergence % and emergence index in all experiments (Mean [range]).

Expt.No.	Seedling emergence %		Emergence index
	Crusted soil	Uncrusted soil	Crusted soil
1	40 [1-66]	65 [11-88]	50 [15-58]
2	36 [7-68]		7 [3-9]
3	26 [1-71]		11 [0-15]

and genotype X experiment interaction had a significant effect on percentage emergence and the emergence index. Genotypes behaved significantly different in different crust situations, however, some genotypes emerged well (more than 50% emergence) in all the three crust situations (Table 3.5 & 3.6).

Table 3.5 Percent emergence of seedlings of some sorghum genotypes.

Genotype	% Seedling Emergence		Crusted/ Uncrusted
	Crusted	Uncrusted	
IS-4474	67	69	0.96
IS-684	52	63	0.83
IS-155	60	69	0.82
IS-3510	59	73	0.80
IS-8962	13	59	0.23
IS-4542	11	49	0.22
IS-4663	7	77	0.09
IS-923	3	40	0.07

Table 3.6 Mean emergence % of some lines showing better emergence in different soil environments.

GENOTYPE	Alfisol field, Patancheru	Aridosol flats, Hissar flats	Alfisol flats Patancheru
	IS-923	87.5	82.0
CSV-5	84.5	89.5	92.5
IS-5140	78.5	70.0	73.0
IS-4667	100.0	84.0	66.0
IS-8962	84.5	80.0	66.0
IS-2314	82.0	86.5	87.5
CSH5	82.0	100.0	92.5
IS-2482	97.5	100.0	77.5
IS 5567	75.5	64.0	77.5
GPR-148	63.0	84.0	87.5
IS-5109	97.5	62.0	92.5
IS-4664	73.5	89.5	99.5
IS-5067	91.0	95.0	96.5
IS-4663	68.0	70.0	63.0
IS-15632	100.0	99.0	96.5
M35-1	89.0	97.5	100.0

The seedlings that emerged on the first day encountered a crust which hardened rapidly. After the first day, the increase in crust strength was less. Hence, the

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seedlings that emerged subsequently were subjected to higher crust strength. Significant genotypic variability was found in emergence percentage based on the number of seeds that did not emerge on the first day. Even after removing the emerging lines which avoided crust, the remaining genotypes also showed significant variability in emergence through soils prone to crusting. Genotypes showing good emergence ability at Patancheru and Hissar were IS 4349, IS 5977, IS 2102, IS 1072, IS 10022, Nagawhite and IS 5642. At Hissar, some lines emerged without the presence of soil crust, while others failed miserably (ICRISAT, 1980).

Although good management practices like use of mulches, chemicals and tillage suggested by some authors (Bansal *et al.*, 1971; Mehta and Prihar, 1973) can improve emergence in an adverse soil environments, selection of lines with the ability to emerge under such situations would be advantageous. It is now important to establish the morphological and physiological characteristics of genotypes which are responsible for the large variation in their ability to emerge through a crust. Thus, genetic improvement for emergence through crust along with improved agronomic practices to reduce crust strength should improve stand establishment in soils prone to crusting. Efforts are required to further simplify methods to develop techniques which would enable the screening of a large number of lines at one time in the field for better emergence under crusting.

Effect of crust strength on radicle and plumule length and percentage emergence of post rainy season sorghum

A tractor mounted planter with a 20 mm chisel furrow-opener was used with the covering wheels. CSH-5, an Indian hybrid was planted at 5 cm depth in moist soil at 14 seeds/m. To induce crust formation, water was applied by a tractor mounted sprayer two days after sowing. There was no difference in radicle length for the crust and no crust treatments. Plumule length were also similar until the start of emergence when the soil crust arrested the rate of plumule elongation in crust treatment (Table 3.7). The penetrometer used to measure crust strength indicated that the lower plumule length and percentage emergence were consequences of the crust since there was no differences in the soil moisture in 0-5 cm layer. Management practices such as mulching and tillage would bring down the crust strength and inherent genetic improvement would further aid in better seed establishment in a crusting soil.

Effect of tillage and genotype on seedling emergence and establishment

Six genotypes showing a range of seedling vigor, 2 each for high, intermediate and poor vigor, were included (Nagawhite, IS 1096, IS 881, CSV5, IS 914, Swarna). Different tillage treatments were applied to prepare the seed bed in black soil, Patancheru (ICRISAT) and seeds were sown at 40 mm depth in each treatment. Different tillage treatments have a significant effect on seedling emergence and early seedling vigor. High seedling vigor lines have shown their superiority in seedling vigor over other lines in all tillage treatments (Maiti and Awadwal - unpublished; Table 3.8).

Effects of methods of providing seed-soil contact on crop establishment

(N.K. Awadwal - personal communication)

Providing good seed-soil contact accelerates seedling emergence. The method for providing seed soil contact is to cover the seed in the furrow with loose s

Table 3.7 Shoot and root growth in crusted and uncrusted fields at Hissar (mean of 26 genotypes).

After	Crusted		Uncrusted	
	20 days	25 days	20 days	25 days
Main root length (cm)	11.3	9.4	12.6	12.0
Shoot length (cm)	13.1	11.5	17.3	14.8
Dry weight (g)	0.12	0.11	0.15	0.14

Table 3.8 Effect of tillage and genotype on seedling emergence and establishment in alfisol. (NS- not significant; * P > 0.05; ** P > 0.01; LSD- least significant difference).

Source of variation	df	F-values (Variables)		
		% First emergence	% Final emergence	Plant height 10 days after planting
Replications	1	1.439 NS	0.109 NS	0.16 NS
Tillage	5	8.124 *	7.428 *	0.249 NS
Genotypes	5	42.628 **	49.782 **	6.132 **
Interaction	25	2.703 **	2.669 **	0.676 **
LSD at 5%				
Tillage	7.84	8.5	0.92	0.71
Genotype	5.81	5.65	0.48	0.94
Within tillage	14.2	13.8	1.17	2.30
Between tillage	15.1	15.1	1.4	2.21

3 levels of pressure). The experiment was done in alfisol with one genotypes, CSH-8, an All India Coordinated Project hybrid. Methods of providing seed soil contact have significant effects on seedling emergence, and also on seedling vigor. Effect of soaking and drying on seed viability

Moreno-L.(1988) demonstrated that some sorghum genotypes had capacity to emerge even after 40 hours soaking in water and drying in the incubator at 15°C for 15 days. These lines could be adapted in dry sowing conditions in semi-arid tropics (Maiti, 1986; Moreno-L., 1988). Later studies have shown that lines resistant to this stress factors contain specific protein of molecular weight of 33.5 kda which is absent or negligible in susceptible lines (Maiti, 1990, unpublished). It was also reported that resistant lines can incorporate higher amounts of amino acids compared to susceptible ones (Sharon *et al.*, 1988). Future studies are needed to confirm whether the specific protein of 33.5 kda is related to resistance under dry sowing.

POST-EMERGENCE GROWTH (SEEDLING VIGOR)

Seedling vigor traits such as dry weight of seed, dry weight of new growth (radicle and plumule), length of radicle and plumule, dry weight of root and first leaf area and total leaf area of seedling, showed variation over a wide range. Different parameters were measured to indicate 1- the proportion of seed reserves mobilized = [Dry weight of seed lost during germination]/[Initial dry weight of seed]; 2- the proportion of mobilized reserves utilized for new growth = [Dry weight of new growth (radicle + plumule)]/[Initial dry weight of seeds 5 days after germination]; 3- the proportion of original seed reserve to new growth = [Dry weight of new growth]/[Initial seed weight].

Different seedling vigor traits showed significant associations among them (Tables 3.9 - 3.10). Genotypes which had more initial seed weight consumed a lower proportion of its mobilized food reserve for new growth, while the genotype which had less initial seed weight (small seeds) consumed relatively higher proportion of its mobilized food reserve for new growth. Therefore, the absolute weight of seed reserve mobilized for new growth during germination and seedling size at 5, 20 and 30 days increases with the increase in seed size. However, the associations between seed size and seedling size at 20 and 30 days after emergence, although significant, are not very strong. In general, big seedlings at 15 and 30 days are produced from big seeds, but not all big seeds produce big seedlings. This is because the photosynthetic area and efficiency of seedlings after emergence influences the seedling growth rate. Seedling size (seedling dry weight) correlated significantly with seed size ($r^2 = 0.61$; Maiti- unpublished).

Table 3.9 Associations among different seedling vigor criteria (36 genotypes). (** P > 0.01).

Traits	1	2	3	4
1-Seed weight (25), g	1			
2-Dry weight of seed lost, g	0.74**	1		
3-Dry weight of new growth, g	0.56**	0.78**	1	
4-New growth/seed lost	-0.38**	-0.42**	0.16	1

Endosperm-dependent seedling growth

In order to assess the effect of endosperm content on seedling growth, 12 sorghum genotypes (IS 7755, IS 7999, IS 11150, IS 4310, IS 3921 and IS 127) were selected for a study. The endosperm was carefully cut to 3/4, 1/2 and 1/4 with a sharp blade without injuring the embryo. Thirty seeds from each treatment were weighed and put for germination testing in petri dishes lined with wet filter paper together with a control (whole seeds). Germination counts were taken after 24 hours and dry weight of seedlings was recorded after 5 days. There were no significant differences among the genotypes, but the endosperm treatment (size) significantly affected seedling size ($P < 0.01$). However, both genotype and endosperm treatment were found to be significantly for dry weight of seedlings at 5 days.

Table 3.10 Correlations (r) among seedling traits (4) (36 genotypes, in wooden flats). (** P > 0.01).

Traits	1	2	3	4
1-Dry wt. of shoot/plant, g	1			
2-Dry wt. of root/plant, g	0.76**	1		
3-Total dry weight, g	0.93**	0.86**	1	
4-First leaf area, cm ²	0.48**	0.48**	0.57**	1
5-Total leaf area, cm ²	0.79**	0.64**	0.84**	0.46**

Relationship between protein content and seedling size

In wheat, high seedling vigor is related to seed protein content (Welch, 1977; Bullisani and Warner (1980). Similar findings were obtained by the author for sorghum (Table 3.11).

Table 3.11 Relationship between protein content and seedling size. (* P < 0.05; ** P < 0.01).

Traits	1	2	3	4	5	6
1-UIR, %	1.00					
2-Protein, %	0.87**	1.00				
3-Seed weight (30), g	-0.48*	-0.61**	1.00			
4-Seedling wt. (30) 5 d.	0.15	0.27	0.08	1.00		
5-Seedling wt./plant, 15 day, g	-0.12	-0.46**	0.63**	0.09	1.00	
6-Total protein content	0.45	0.51	0.35	0.46*	0.11	1.00

Seedling vigor in laboratory and field tests

The dry weight of seedlings sown in the laboratory showed significant positive correlation with dry weight of seedlings sown in the field. To standardize a laboratory test that may be used as a preliminary indication for the evaluation of seedling vigor, regression analyses were attempted for the dry weight of seedlings grown in the laboratory and in the field. The analysis established a significant relationship between the dry weight of field shoot at 30 or 20 day and dry weight of new growth on the fifth day in the laboratory. These results indicate that laboratory tests may help as a preliminary screening method for the evaluation of seedling vigor under field conditions.

Evaluation of seedling vigor

There are 2 important aspects of seedling vigor in sorghum: 1- the ability to establish a satisfactory stand under a variety of conditions, and 2- the ability to

produce rapidly growing seedlings. Work done in this area has largely concentrated on stand establishment and relationship of seed characteristics, seed size, laboratory tests for vigor, and to field establishment. Initial work on seedling vigor by the author at ICRISAT concentrated more on the seedling size/growth rate aspects of vigor. This was partly in response to the large variation in seedling growth rates that were evident in the breeding materials and germplasm collections. It was also based on the assumption that large, vigorous seedlings perform better over a wide range of seed-bed and environmental conditions and need to be researched for genetic improvement for sorghum crop adaptation.

Seedling size or growth rate is best assessed by direct measurement of seedling weight and leaf area. For evaluation of seedling vigor, direct measurements approximately 15 days after emergence are used in genotype comparison. However, this is a laborious and time-consuming process when a large number of genotypes are involved. The present study was undertaken to evaluate how effective is visual scoring for seedling size is, and how closely visual scores are related to measured seedling dry weights and leaf areas (Maiti, 1981). Seedling size in a variety is largely determined by edaphic conditions and soil fertility. Therefore, to evaluate seedling vigor of a set of genotypes, we need to grow these seedlings in a precision field with uniform fertility. This simple non-destructive technique could be used in the evaluation and improvement of seedling vigor in segregating generations in a breeding program.

Sorghum lines with improved seedling growth rate have been shown to be more competitive with weeds (Guncelyi *et al.*, 1969). No study directly links seedling size to final crop performance in sorghum, although seedling size/dry weight has been reported to be positively correlated to grain yield in oats (Bain *et al.*, 1969) and barley (Singh *et al.*, 1975). Lawrence (1963) has standardized different methods for evaluation of Russian wild rye grass for seedling vigor. He suggested selecting large-seeded lines and selecting them for deep seeding is a suitable method of incorporating seedling vigor in a breeding program.

Visual rating of seedling vigor

A wide range of seedling vigor has been reported in sorghum (Maiti, 1981). Differences in height, leaf breadth, leaf number and pseudostem thickness were evident in sorghum germplasm belonging to different taxonomic groups. Visual scores were compared to measured dry weight per seedling for their ability to distinguish among genotypes by computing ANOVA tables for genotypes. Visual score at 7 and 11 days, and dry weight at 15 days. Research at ICRISAT has shown that 15 days after emergence, genotypes are generally variable in the expression of seedling vigor (Maiti, 1981).

Relationship of visual score to dry weight and leaf area

The relationship of the visual score to actual seedling growth and leaf area was examined in a set of 50 genotypes. All correlation coefficients were highly significant (at 1% probability). Leaf area and dry weight were also very closely linearly related in these lines (Tables 3.12 - 3.13). To understand if the relationship between visual score and seedling dry weight is a result of interaction of genotype differences for height and maturity, 22 dwarf germplasms belonging more or less to the same maturity group were evaluated. It was found that visual scores show

a significant relationship with seedling dry weight ($r^2 = 0.92$).

Table 3.12 Comparison of visual scoring to dry weight determination for seedling vigor assessment (512 genotypes; Maiti, 1981).

Traits	F ratio	CV	LSD 5%	Range	Mean
Visual score 7 days	2.93 **	14%	1.2	1-5	3.2
Visual score 14 days	2.03 **	18%	1.5	1-5	3.0
Dry weight per plant (g) 15 days	1.76 **	27%	0.4	0.14-1.24	0.46

[** P < 0.01]

Table 3.13 Correlations among seedling vigor estimates (50 genotypes; Maiti, 1981). All coefficients significant, P < 0.01.

Traits	1	2	3	4
1-Visual score 7 days	1.00			
2-Visual score 14 days	0.84	1.00		
3-Dry weight 15 days	-0.76	-0.82	1.00	
4-Leaf area 15 days	-0.81	-0.87	-0.90	1.00

Comparison of criteria for estimating seedling vigor

The visual score was compared to measured dry weight per seedling (at 14 and 15 days) for its ability to distinguish among genotypes. F ratios for genotypes were not different for visual score and dry weight, but the coefficient of variation for the visual score (14 and 18%) was lower than that for the measured dry weight (27%). Similarly, the ratio of the range of the measured variable to the LSD was better in the case of visual score (4.2 and 3.3) than in the case of the actual seedling dry weight (2.8) (Maiti and Bidinger, 1979; Maiti, 1981).

The visual scores should be effective in distinguishing genetic differences in seedling vigor in sorghum. For routine breeding work however, scoring should be quite efficient, specially in that the range of scores is approximately three times the LSD. Visual scores are well correlated to the direct measures of seedling vigor and are effective tools for distinguishing genetic differences among a large number of entries. A large number of lines can be scored easily and rapidly by using this technique which suggests that this could be routinely incorporated into a breeding program where seedling vigor is an important attribute. Studies at ICRISAT have indicated that seedling vigor is correlated to its emergence ability through crust and drought resistance at the seedling stage (ICRISAT, 1980). Therefore, the performance of high seedling vigor lines under adverse conditions needs to be tested.

The only limitation of the visual scoring method is that direct comparisons between experiments, generations, etc., may not be possible, although comparisons could be made. But this should not be considered a serious limitation as the main objective of the breeding program is usually the selection of the individuals from a group of entries handled and tested as a unit (Maiti, 1980). Crosses (F3 population) between seedling vigor source and a range of parents (Maiti - unpublished)

It is interesting to study how seedling vigor behaves in parents and their progenies. Sixty-six crosses were made at Patancheru, ICRISAT, between Nagawhite (with extraordinary early seedling vigor) and a range of parents from NP, WAB and bulk Y were evaluated in the field.

Similar type of associations were observed as in the previous studies. The weight of seedling at emergence showed significant positive correlation with dry weight of seedling at 15 days. On the basis of this study, 28/66 entries were found to be superior to Nagawhite at emergence and at 15 days after emergence. At 15 days after emergence, entries with seed size less than that of Nagawhite were all inferior in performance. Using the measurement made on the 66 crosses between Nagawhite and a range of parents from NP, WABC and bulk Y, it appears that the evaluation and selection for good seedling growth (regardless of yield) could be based on: 1- dry weight measurement at 7 or 15 day stage to ensure that vigor is not ephemeral, while taking into consideration differences in area and or photosynthetic efficiency of leaves; 2- seed size having selected genotypes based on seedling size, these may be grouped into: a) genotypes with seedling size and seed size equal or greater than the check, and b) same as but the seed size smaller than the check.

Relationship between seedling vigor with the total biological yield

The yield components of 66 crosses and Nagawhite (high seedling vigor) and CSH-1, an Indian hybrid, were taken in separate experiments. Seedling weight at 15 day (seedling vigor) was found to correlate with the final plant height ($r = 0.4$, $P < 0.01$), total dry weight ($r = 0.4$, $P < 0.01$) and weight of seedling panicle. Plant height again was found to be associated with grain weight ($r = 0.4$, $P < 0.1$) but not with grain weight ($r = 0.4$, $P > 0.01$). In this experiment (F3 progenies of Nagawhite X, Bulk Y and WABC) seedling vigor was found to be associated with their good performance in respect of yield components and yield. The study indicated that the bigger the seedling size (at 15 days after emergence), the higher the total (biological) yield, although this may not apply to all big seedlings. However, higher seedling growth may not necessarily lead to higher economic yield, because the characteristic determinants of seed number have to make a complementary contribution if rapid and high growth rate during seedling development stage is to result in increased yield (Maiti, unpublished).

The higher the leaf area at emergence, the bigger the seedlings at 15-20 days after emergence. Furthermore, as soon as the seedling becomes autotrophic, total and leaf growth rates depend on the photosynthetic efficiency of its leaves which at emergence, are larger in the large seeded genotypes. Therefore, seedlings from a genotype whose initial seed weight is less than the check could partially

compensate for the disadvantage in seed size, although this may not happen. The selected genotypes have also been tested for yield. The material with vigor greater than the original parent crossed to Nagawhite indicated that enough improvement was achieved both in seedling growth and yield. The materials with yield lower than the original parents crossed to Nagawhite obviously had significantly reduced seedling vigor, but they may be maintained as a source material for further use in population or crosses. It is assumed that this may be put together in a population which included the early seedling vigor, a GS2 with a partitioning of the photosynthates and the nutrients which favored the developing panicle and plants with a GS3 having a longer than usual duration of grain-filling coupled with a higher rate of filling. We might get a recombination from such a population which would show improved yield. Research effort needs to focus in this direction.

Factors controlling seedling vigor in sorghum

Where seedling vigor is a breeding objective, evaluation of seedling vigor in a crop must be done under constraints other than those that affect the evaluation of vigor in commercial seed lots. A breeding line is often represented by a few panicles, a single panicle, or even a plant. Successive generations may be produced under very different environmental conditions, particularly where off-season nurseries are employed. With certain crops, only selected portions of the reproductive structure(s) may be harvested for generation advance. How these constraints affect the results of seedling vigor evaluations - or if they are important at all - is largely a matter of conjecture.

All these constraints exist for sorghum (*Sorghum bicolor* L. Moench). Head to head selection is the common practice in both pedigree breeding and in male-sterile-based population breeding systems. Two generations per year are grown in programs where alternate locations (temperate zones) or irrigation facilities (tropical zones) are available. Finally, it is a common practice to remove the frequency of outcrossing when the panicle is not bagged.

The existing literature on seedling vigor in sorghum deals mainly with the role of seed size in germination, field establishment and seedling size. Seed-lot comparisons have demonstrated that larger seeds generally have a superior germination than standard germination (Abdullahi and Vanderlip, 1972; Maranville and Clegg, 1977). However, field establishment is not always superior in larger sized seeds (Abdullahi and Vanderlip, 1972; Suh *et al.*, 1974; Maranville and Clegg, 1976). Similarly, seedling size (or growth rate) was not related to seed size (Suh *et al.*, 1974). Similar results have been reported from comparisons among cultivars (Swanson and Hunter, 1936), and for comparisons of different seed lots of the same cultivar (Abdullahi and Vanderlip, 1972). In neither case were demonstrable differences among cultivars/seed lots related to seed size differences. Maiti and Carrillo (1991) reported that sorghum genotypes showed variability in seedling emergence from deeper planting depth, and the capacity of emergence from deeper planting is associated with the capacity of elongation of mesocotyl from deep planting.

The objective of these studies were to: 1- evaluate the effects of the constraints on seedling vigor evaluation on the results of vigor evaluation tests, and 2- to test the effects of seed size differences in seedling vigor in these comparisons.

The specific comparisons made were as follows : 1- variation in vigor among seeds from individual panicles of the same cultivar, 2- variations in vigor among seeds from large and small panicles of the same cultivar, 3- variations in vigor among seeds from the upper, middle and basal portions of the panicle, 4- effect of nitrogen fertility during seed production on seedling vigor, and 5- effect of water stress during seed production on seedling vigor (Maiti, unpublished).

Most of these studies made use of existing seed lots or existing experiments from which seed samples could be harvested for specific comparisons. These cultivars and lines used differ between comparisons, as do sample sizes used in estimating seedling emergence and seedling vigor. Comparisons between individual experiments should be made with this caution.

Evaluation of vigor

Seedling vigor was measured first by counting the number of seedlings emerging from a standard number of seeds sown, and second, by measuring the total above ground dry weight for a standard number of seedlings, 15 days after seedling emergence. The tests were conducted in wooden flats, 110 X 60 X 22 cm, filled to a depth of 17 cm with field soil. The soil used was a vertisol (black soil) which had been ground, mixed and fertilized with the equivalent of 45 kg/ha of nitrogen and phosphorous (calculated on a surface area basis). Two seeds were sown per hill at a depth of 3 cm, with hills spaced at 10 cm intervals. Furadan was applied with the seed to provide protection against the sorghum shootfly (*Antheraea soccata*) as the tests were conducted under natural environmental conditions.

Seed source

All comparisons were carried out on seed from pure line cultivars to minimize genetic differences among individual seeds or seedlings. The rationale in so doing despite the fact that the studies were done to provide information on seedling vigor evaluation in breeding materials (including segregating materials), was as follows: if differences in seedling vigor among panicles, seed lots, etc., exist where the genetic variation among these is supposedly at a minimum, then such differences would be important as possible confounding factors in cases where genetic differences among these factors were the object of selection. Various comparisons were made on seeds from individual panicles or from bulk seed lots as appropriate to the comparison. The former source was used for the comparison of panicle to panicle variation and within panicle variation, and the latter for testing the effects of environmental influences during seed production. Generally, seed used was not from selfed panicles but as outcrossing in sorghum is considered to be less than 5% (Doggett, 1970), this was not considered to be a serious problem. Specific details of how seed for the individual comparisons was selected is described in the following sections.

Panicle-to-panicle variation

Ten panicles in sequence (approximately 1.5 m row) were collected and threshed separately from each of 3 cultivars (M35-1, CSV3 and V302) from irrigated summer season (Feb-May) planting in India. There were significant differences among the seed samples from individual panicles in seed size and number of seedlings emerged, but no differences in seedling size (Table 3.14). There was no evident association between differences in seed size and differences

in emergence for any of the cultivars. Thus, these results agree with those of Abdullahi and Vanderlip (1972) in that differences in emergence within a cultivar are not dependant on seed size.

Table 3.14 Plant to plant variation in seed size and seedling vigor.

Cultivar	Seedling wt. g/30 seeds		seedlings/ 6 seeds		g dry matter/ 3 seedlings	
	Mean	Range	Mean	Range	Mean	Range
M 35-1	1.21	1.02-1.32	5.4	4.7-5.8	0.79	0.70-0.83
CSV3	0.74	0.63-0.92	5.4	4.3-5.9	0.37	0.32-0.43
V302	1.18	1.04-1.29	5.4	4.3-6.0	0.79	0.71-0.89

An additional sampling was carried out to determine if these differences in emergence among seed samples from different panicles were related to differences in parent plant vigor (estimated by the size of the panicle produced by the plant). Five panicles, each from arbitrarily defined large and small panicle - size classes were randomly selected from 5 cultivars (M35-1, CSV3, V302, Patancheru local and IS 1037), taken from the same experiment as the previous sampling. Seed weight and seedling vigor were estimated as in the previous comparison (except that four seeds rather than eight were sown per replicate). There were no differences in either of the three variables measured between the large and small panicle size classes, although individual panicles were significantly different for all parameters.

Within-panicle variation

Five individual panicles each of 4 cultivars (IS 7880, IS 3921, IS 4850 and IS 7755) were randomly selected from an irrigated summer season planting. Each panicle was divided into upper, middle and basal portions, by dividing the rachis into 3 approximately equal segments. Seeds from individual panicles differed in emergence and in seedling size, but there was no effect of location of seed on the panicle on seedling vigor or seed size. Thus the practice of clipping the upper portion of the sorghum panicle following anthesis would not appear to introduce bias in seedling vigor estimates, unless there are genotype X clipping treatment interactions (which were not evaluated). It is feasible to use the seed from the upper portion of the panicle for estimating seedling vigor where selection for vigor on an individual panicle basis was the objective and retain the remaining seed for resowing the lines selected for advancement.

Effects of environmental conditions on seed production

Bulk seed samples from experimental test cultivars under high and low nitrogen fertility conditions and drought stress conditions were used to test the effects of seeds produced in these conditions, on seedling vigor. The seeds for the nitrogen fertility comparison were produced in post-rainy season (October-January) crops fertilized with 100 and 20 kg/ha nitrogen for the high and low fertility comparisons

respectively. Eight cultivars were used in the study: GPR 148, Q1689, P721, M316-S, Q2959, CSH1, CS 3541 and M35-1. Seed weight seedling emergence and seedling size as the dry weight were estimated. The seed for the drought stress effects test was produced in an irrigated dry season planting in which the cultivars used (IS 1037 and V302) were grown under a fully irrigated (no stress) and stress treatments (effected by withholding irrigation) of approximately 25 days duration just prior to flowering and during the grain filling period. Seed weight, seedling emergence, and seedling dry weight were estimated.

Seed size in the low nitrogen treatment was less than in the high nitrogen treatment (Table 3.15), but the effect was mainly due to two cultivars, CSH1 and M35-1. Seedling size from seed produced under low nitrogen fertility conditions was also less than that from seeds produced under high nitrogen fertility conditions; and cultivar X treatment interactions were significant. Seed size was reduced by both moisture stress treatments although to a much greater degree in the grain-filling stress, as expected; it was also reduced in the case of seeds produced in the grain-filling stress, but not in the case of seed produced during the pre-flowering stage. Seedling emergence was unaffected by either nitrogen or moisture stress conditions (Table 3.16).

Table 3.15 Effects of high (HF, 100 kg/ha) and low (LF, 20 kg/ha) nitrogen fertilization during seed production generation on seed size and seedling vigor.

Cultivar	Seed weight g/30 seeds		Emergence seedlings/12 seeds		Seedling weight g dry matter/6 seedlings	
	HF	LF	HF	LF	HF	LF
GPR 148	0.83	0.85	10.7	11.8	0.65	0.84
Q 1689	0.80	0.77	10.9	10.2	0.77	0.68
P 721	0.67	0.72	11.5	11.6	0.79	0.69
MYX 316-S	0.79	0.73	11.6	11.8	0.97	0.72
Q 2959	0.95	0.87	11.9	11.8	0.90	0.71
CSH-1	1.25	1.15	11.2	11.9	1.09	1.04
CS 3541	0.88	0.82	11.7	11.4	0.72	0.55
M 35-1	1.24	1.13	11.0	11.3	0.82	0.95
X	0.93	0.88	11.3	11.4	0.84	0.77

The results indicated that genotypic evaluations of seedling vigor (seedling emergence or growth rate) should be made only on seed samples produced under the same conditions. The evidence of genotypes X environment interactions for the nitrogen fertility comparison suggests that even enhancing evaluations to a common check cultivar for across-location, across-year or across-generation comparisons is open to question. This caution does not pose a problem for routine relations of seedling vigor, as a given set of breeding lines are usually grown and handled in a uniform manner for other reasons. This caution is important, however, in studies of the inheritance of seedling vigor or in estimating genetic advance made by selection

for vigor. In the latter, it may be necessary to specifically produce seeds for such tests under uniform conditions, rather than relying on remanent seeds as is frequently done for measuring effects of selection on yield, diverse resistance, etc.

Table 3.16 Effects of water stress (S) compared to nonstress (NS) during seed production generation on seed size and seedling vigor.

Stress	Seed weight g/30 seeds		Emergence seedlings/12 seeds		Seedling weight g dry matter/6 seedlings	
	S	NS	S	NS	S	NS
Pre-flowering						
Cultivar	S	NS	S	NS	S	NS
IS 1037	0.95	0.97	39.2	39.6	1.90	1.92
V 302	0.93	1.10	38.0	37.8	1.65	1.61
Mean	0.94	1.04	38.6	38.7	1.78	1.76
Post flowering						
Cultivar	S	NS	S	NS	S	NS
IS 1037	0.60	0.97	38.4	39.6	1.40	1.92
V 302	0.65	1.10	38.4	37.8	1.20	1.61
Mean	0.62	1.04	38.4	38.7	1.30	1.76

Variability for different crop establishment traits

A set of 100 lines and 2 checks which were basically selected for individual traits, were tested for different crop establishment traits, e.g. emergence under optimum soil moisture, emergence through crust, seed viability following wetting and drying, seedling vigor and drought at the seedling stage. There was a wide range of variability for different traits. A set of 102 sorghum genotypes were evaluated for different crop establishment traits, e.g. soil temperature, viability of seeds, planting depth and seedling vigor (Maiti, 1986). A varying potential for resistance to one or more adverse factors exist in known sorghum genotypes.

Conclusions

The results on seedling emergence and seedling vigor in sorghum could be summarized as follows:

1. Genotypes show many variations and offer much scope in genetic improvement for better emergence and vigor by selection.
2. Different seedling vigor traits show good associations among themselves.
3. Laboratory evaluations of seedling vigor have shown some degree of correlation with field evaluation. Initial evaluation in the laboratory may give some indications about field performance.
4. Seedling vigor is found to show significant positive associations with total biological yield.
5. Visual scoring system may be conveniently adopted for seedling vigor evaluation as it correlates significantly with seedling dry weight and leaf area.
6. Depth of planting and endosperm content have significant effect on seedling vigor but seed size has little or no effect on it.

7. It was possible to screen genotypes for emergence ability through adopting a suitable method. The genotypes have shown significant variability in seedling emergence through crust.
8. Within and in between genotypes, variations and environmental factors found to influence seedling vigor. Though seed size has little or no effect on seedling vigor, genotypes have a major effect on seedling vigor. This needs to be taken into consideration in seed production program.
9. There exists a varying potential for resistance to one or more seedling establishment traits in sorghum.

DROUGHT RESISTANCE AT THE SEEDLING STAGE

Even after good emergence, seedlings may undergo long periods of dormancy before the next rains. To understand the factors affecting seedling establishment attempts have been made with different crops to develop techniques to improve germination and early seedling growth under water stress (Nour *et al.*, 1978; Pooler and Pfeifer, 1956; Sammons *et al.*, 1978, 1979; Sharma, 1973, 1976). Polyethylene glycol solutions of known osmotic pressure have been widely used to study germination differences (Uhvits, 1946; Williams *et al.*, 1967; Saint-Clair, 1976; Sharma, 1976). Solutions with different osmotic pressures have been reported to have specific effects on germination, independent of water potential (Parmer, Moore, 1968; Sharma, 1973; McDonough, 1976). Selection of drought resistant lines in winter wheat was made by Powell and Pfeifer (1956) using controlled moisture systems. A cellulose acetate membrane separating a polyethylene glycol solution from the soil was modified by Douglas and Asay (1978) to evaluate seedling emergence. This technique eliminated contact of seed and osmoticum, thus permitted a wide range of soil water potentials. Attempts to screen soybean lines in growth chambers were not successful (Sammons *et al.*, 1978) but screening in drought boxes produced better results (Sammons *et al.*, 1979). The percentage of sorghum seedlings surviving after repeated drought stress was found to be a useful index for selection (Nour *et al.*, 1978). The technique of growing sorghum seedlings hydroponically with added polyethylene glycol-600 in dish - pans was examined by Sullivan and Ross (1979). When the seedlings were 7 to 10 days old, Carbowax 600 was added to the solution in increments over a three-day period until a stress of -15 bars was reached. With sorghum, few researchers have been successful in establishing a good technique for seedling drought resistance (Nour *et al.*, 1978). Drought resistance at later stages in general did not correlate with resistance at later stage of development (Williams *et al.*, 1967; Kilen and Andrew, 1969). This needs to be confirmed in future research.

Although the seedling screening procedure adopted earlier appeared to be simple, cultivar differences in drought response, these procedures were not simple (Sullivan and Ross, 1979). The relatively sophisticated instrumentation and apparatus used were cumbersome for mass screening of a large number of germplasm lines (Sammons *et al.*, 1978, 1979). The usefulness of different techniques for evaluating seedling drought resistance in sorghum is discussed here. The techniques adopted are less complex than those used earlier (details of the techniques

discussed in the appendix). At ICRISAT, the author was actively involved in developing experiments to evaluate sorghum genotypes for drought resistance at the seedling stage in the field and in semi-controlled condition in flats and greenhouses (Maiti & González, 1989).

In all the experiments, limited water (40 mm) was given once following sowing with no further watering until the seedling showed severe wilting. As the seedlings grew in the depleting soil moisture, drought symptoms were gradually noticed. First, the seedling leaves showed rolling which is a mechanism to close stomata to reduce transpiration; leaf rolling thus seems to reduce the effective leaf area per plant (Blum, 1974a, 1975a). Some genotypes showed wilting quite early and reached the permanent wilting stage: they did not regain turgor during night and early morning. Some lines did not show wilting under the same level of soil moisture and maintained turgor; this might be due to higher leaf water potential, the characteristic of drought resistant lines described by Blum (1974a, 1975a). As soil moisture stress increased, seedling growth slowed relative to the degree of tolerance of the tissue to drought (Blum, 1979a). When it was assessed that more than 50% of the genotypes would recover after release, the field was rewatered. Some genotypes recovered early, and some long after release of water stress. Visual scores for wilting and recovery (1 = best, 5 = poorest) and recovery percentage were taken as indices of drought-resistance. The experiments revealed that genotypes did differ significantly in different drought resistance indices.

The experiments were complementary to each other. In the wooden flats, the competing lines were submitted to stress at the same time. A better water-use efficiency mechanism in a particular line may not be of any use in delaying the stress, because of the competition with the neighboring line for less water conserving capability. If a line has been able to survive, it was because it was able to withstand the stress better rather than its ability to delay the onset of stress. In the PVC cylinders the lines are isolated and if they are more efficient in water use, they can delay the onset of stress; if they have a built-in tolerance mechanism to withstand the stress better, they can survive still longer.

Considering CV% and LSD, seedling drought evaluation in PVC cylinder in glass house was better than in any other technique, although each technique had some drawbacks. The correlation coefficients between different drought response indices for different techniques are given in Table 3.17. The high degree of association between different seedling drought parameters indicates that visual score for wilting and recovery score could be considered as reliable parameters in the screening of genotypes for seedling drought resistance. Seedling vigor (dry weight of seedlings) did show significant positive correlation with seedling drought resistance parameters (visual score for wilting, $r = 0.67$; plant height, $r = -0.50$; $P < 0.01$). This indicated that seedling vigor is related to some extent to seedling drought resistance (Maiti and González, 1989). Several germplasm and breeder lines were selected for a high level of drought resistance at the seedling stage. These were IS 2146, IS5604, IS 3962, IS 1096 and (breeding) D 719114, D 71914, D 719, IS 7389, IS 7389, D 71873, D 71824 and BG 74.

Table 3.17 Correlation coefficients among different drought parameters (ICRISAT, 1980). (** P < 0.01).

Parameters	Wooden flats	PVC-cylinder
Visual score for wilting vs recovery score	0.73 **	0.90 **
Visual score for wilting vs % survival	-0.74 **	-0.90 **
Recovery score vs % survival	-0.89 **	-0.99 **
Visual score for wilting wooden flat vs PVC cylinder		0.65 **
Recovery score wooden flat vs PVC cylinder		0.56 **

Table 3.18 t-test between eight glossy and eight non-glossy lines in different seedling drought tolerance parameters using different techniques.

Parameters	Glossy	Non-glossy	t-value
Wooden flats			
Visual score for wilting	2.28	3.50	4.01 *
Recovery score	2.62	3.37	1.96 NS
Percent survival	70.52	48.85	2.45 *
PVC cylinders			
Visual score for wilting	1.75	4.00	6.42 **
Recovery score	1.91	3.69	5.34 **
Percent survival	80.21	39.58	4.22 **
Field			
Visual score for wilting (35 days)	2.62	3.62	1.86 NS
Plant dry weight (35 days)	3.33	2.90	0.97 NS
Plant height (30 days)	25.17	20.03	1.99 NS

(NS= not significant; * P<0.05; ** P<0.01; scores: 1=best, 5= poor).

Differential response of glossy and nonglossy lines to drought resistance at seedling stage

In the experiments to evaluate seedling drought resistance, the lines with glossy leaf characteristics were more resistant to drought than the non-glossy ones. In a field experiment that adopted cluster analysis, it was observed that 87% of lines falling in the best group in cluster 1 had glossy leaf surfaces, while 100% of the susceptible lines forming cluster 4 were non-glossy. In all these experiments the glossy lines showed statistically significant differences from the nonglossy lines in different drought resistance characteristics (Maiti, 1986).

When stressed for water, a set of 12 lines (7 glossy and 5 nonglossy) showed significant differences ($P < 0.01$) in their leaf water potential measured 30 days after emergence. In one of the experiments, stomatal resistance recorded 34 days after emergence showed that the glossy lines had higher resistance compared to the nonglossy lines (glossy 6.9 ± 3.8 sec/cm; nonglossy 5.6 ± 1.8 sec/cm). However, leaf temperatures were the same ($31 \pm 0.7^\circ\text{C}$). At the seedling stage, the glossy lines were found to lose less water through transpiration than the nonglossy lines. This was more pronounced up to 11 days.

Seedling growth was generally found to be retarded under water stress in both glossy and nonglossy lines. However, the change in the rate of dry matter accumulation was less in glossy than in nonglossy lines, which indicated that the seedlings of the glossy lines were better adapted to survive drought conditions.

At 22 days of growth there were little differences in the leaf areas of the glossy and nonglossy lines. Thereafter, this factor was not the one responsible for lower transpiration. There were no big differences in root and shoot lengths between the glossy and the nonglossy lines. Although the root length and leaf area of the glossy lines were at par with the 'nonglossy' lines, the water use efficiency of

Table 3.19 Water use efficiency (WUE, g total dry matter/lit water transpired) of glossy and nonglossy sorghum (IS= glossy).^a

Sorghum EXP. # 1	WUE	Dry Weight (g)		Shoot/Root Repts.	
		Shoot	Root		
IS-2394	14.6	8.4	2.0	4.2	5
IS-3962	17.3	15.1	3.6	4.2	6
IS-4405	9.0	16.4	4.4	3.7	2
RS 671	12.2	21.6	5.0	4.4	6
CSV5	11.4	11.6	3.4	3.4	6
4449	9.9	11.4	3.5	3.3	6
15701	10.0	11.6	4.6	2.5	2
6205	8.9	14.8	5.3	2.8	3
EXP. # 2					
IS-5567	13.9	14.6	4.8	3.1	6
IS-4405	7.1	12.8	6.4	1.9	4
IS-4621	9.7	20.7	7.3	2.8	2
IS-1096	11.4	15.1	5.3	3.0	4
9040	6.4	11.1	7.0	1.7	6
226	9.0	18.9	7.6	2.5	6
RS 671	10.0	18.2	7.6	2.6	5
15701	9.6	21.8	8.5	2.6	1

a) Plants were grown hydroponically in plastic cylinders (15.4 X 7.7 cm.). In the first experiment, the plants were harvested at 72 days after germination. In the second experiment, the plants were harvested 63 days after germination.

glossylines was significantly higher in terms of water required to produce one gram of dry weight, compared to the nonglossy lines ($P < 0.01$, Table 3.18). Reduced transpiration and high water use efficiency might be an adaptation to drought situations.

In a study in solution cultures by Sullivan and Maiti (unpublished) glossy lines showed higher water use efficiency compared to nonglossy (Tables 3.19, 3.20).

Some nonglossy lines (e.g., IS 6077 and IS 7503) showed almost the same level of resistance as the resistant glossy lines. The drought resistant nature of nonglossy lines may be attributed to root system, vascular structure, stomatal resistance and some other traits which need to be thoroughly investigated. Therefore, recombination of the resistant glossy and nonglossy lines may improve the breeding approach to evolve drought-resistant strains. The mechanism of resistance in the glossy lines needs to be investigated. Reflectance of sunlight leads to drought resistance. Under a scanning electron microscope (SEM) the glossy crystals were large and flat in shape, whereas nonglossy lines showed no smooth wax and presence of small needle shaped crystals (ICRISAT, 1980; Maiti, 1983).

Saucedo-Rodríguez (1985) showed that there was large variability among sorghum genotypes in resistance to drought which could be correlated with transpiration rate and some biochemical traits (e.g. chlorophyll, carbohydrate, and HCN content). Resistant genotypes showed concentration of these compounds. With an increase in water stress there was gradual increase in carbo-

Table 3.20 Visual rating for drought tolerance of glossy and nonglossy sorghums.

Sorghum	Replications (9 plants each) §				Mean
	1	2	3	4	
IS-1096	1.5	2	3.5	2	2.3
IS-462-1	4-	4	3	5	4.0
IS-3962	1	1	2	3	1.8
IS-4405	2	2	3	2	2.3
IS-2394	4	4	3.5	4	3.9
IS-5567	4-	4	4-	4	4.0
RS-671	5	5	5	5	5.0
4449	2	3	2	2.5	2.4
15701	3	2.5	0	4	3.2
CSV5	3+	3+	3+	3	3.0
6205	3	3	3-	4-	3.3

§ Ratings were 1 to 5, where 1 = green plants, in good condition, 2 = some plants or leaves showing injury, but remainder of plant was green; 3 = about half of plants or plant leaves with dead or dying leaves; 4 = severe drought injury, about 1/4 or less of plant with green leaf tissue; 5 = dead plants. 0 = indicates no plants in that replication.

Drought stress was induced by additions of polyethylene glycol 8000 added to the nutrient solutions in which the plants were growing, beginning at 7 days age. The drought stress was gradually increased to -14 bars at 17 days age. Rating § was done at 21 days.

hydrate, wax and HCN contents, but with a decrease in chlorophyll content, subsequently. Terán-H. (1990) reported that there existed significant difference among sorghum genotypes for resistance to drought and also to salinity, showing high genetic advance for some of the stress resistance variables. Some lines were selected to be tolerant to drought and salinity.

Ramírez-Sarquis (1988) showed that glossy sorghum showed higher amount of root resistance to drought at the seedling stage. Glossy lines showed a consistent advantage over nonglossy under short water supply and higher capacity to survive under severe drought and to recover and resume growth sooner than nonglossy lines; glossy lines had higher root systems than non glossy ones (Ramírez-Sarquis, 1988).

Relationship between resistance at the seedling stage and at advanced growth stages

Genotypes that are drought resistant at the seedling stage and which also show a reasonable level of resistance at advanced growth stages need to be identified. Some of the selected lines gave reasonable yields both under irrigated and non-

Table 3.21 Yield (kg/ha) of genotypes (selected for drought resistance at the seedling stage) under control and stress (CSH6, CSH8 = checks). Post rainy season, 1980.

Genotypes	Control	Stress
IS-2122	3467	2100
IS-4473	3200	2733
IS-5567	4717	3233
IS-4776	3000	3083
IS-5067	4883	3133
IS-5621	4917	2317
IS-1054	5183	2983
IS-2394	4967	3233
IS-4712	4183	2617
IS-2314	5033	2500
IS-1096	4617	2900
IS-4663	5667	2417
IS-923	4717	2183
IS-2280	4967	2750
IS-5633	4750	2133
IS-4405	3867	3767
IS-5642	5250	2517
IS-8311	2917	2250
IS-2146	4850	2283
CSH-6 (hybrid)	5133	3800
CSH-8 (hybrid)	7233	3017
SE of the mean	214	109
CV %	21	18

irrigated treatments (2900 to 5700 kg/ha in irrigated, and 2100 to 3800 kg/ha in non-irrigated plots). The yields of IS 4405, IS 2394, IS 1696 and IS 5567 were comparable to the two standard hybrid checks, CSH-8 and CSH6. This study indicated that selection for drought resistance at the seedling stage might result to some extent its performance at advanced growth stages (ICRISAT, 1980; Tahir, 1983; 3.21).

Seedling vigor (seedling size) was found to be significantly correlated with emergence through the crust stage. The glossy lines IS 4663, IS 5484 and IS 5567 showed reasonable resistance to soil crust and drought at the seedling stage as well as to shootfly (multiple resistance) (ICRISAT, 1981).

In conclusion, we may state that the experiments so far developed to identify genotypes resistant to drought show satisfactory results but need to be improved. Once an effective technique is standardized, the loss in yield because of drought can be minimized. Under conditions of severe drought, different genotypes may decrease their yield due to the effect of drought in varying degree; some genotypes give a reasonable yield under drought as well as under irrigated conditions, having an overall high average. These genotypes could have potential both under favorable and unfavorable moisture conditions. Now physiologists and breeders are working together to identify characteristics related to drought resistance and to venture to create genetic diversity. If a simple morphological trait is found to be associated with drought resistance, it would simplify the breeding procedure. The glossy trait in maize is found to be related to drought resistance, and is a simple inherited trait. The identification of glossy trait in sorghum and its relation to drought resistance may help sorghum breeders incorporate this trait into elite lines for genetic improvement of drought resistance (Maiti, 1986).

SEEDLING MORPHOLOGY

Sorghum germplasm at the seedling stage can be distinguished into 2 distinct morphological types: 1) 'glossy', and 2) 'nonglossy'. The glossy lines have light green leaves with shining appearance. The shining surface is clearly reflected on a sunny day, and the appearance is more distinct at an early seedling stage when the glossy trait appears. This varies with genotype. In a few genotypes, it appears quite early, even at emergence, while in others it appears quite late, i.e., after about 20 days. Scores on a 5-point scale could be given to glossy lines in decreasing intensity of leaf color and shining leaf surface.

Glossy lines accounting for less than 1% of sorghum germplasm are mostly of peninsular Indian origin, others originate in African countries such as Ethiopia, Nigeria, northern Cameroon and Republic of South Africa. The glossy lines play an important role in sorghum crop improvement.

Though pigmentation and tillering differences are observed at the seedling stage between lines, they tend to vary with season. In post-rainy season, tillering is high and the low temperatures seem to enhance purple pigmentation at the seedling stage. Phosphate deficiency sometimes induces purple pigmentation at the seedling stage.

Within the glossy and nonglossy lines, depending upon the nature of the canopy and the pseudostem, the lines may be further classified into erect and pendant subclasses. The size of leaves enables us to distinguish two morphological groups, broadleaved and narrowleaved, from each subclass.

SORGHUM GERMPLASMS (SEEDLING MORPHOLOGY)

GLOSSY		NONGLOSSY		
ERECT	PENDANT	ERECT	PENDANT	SEMI-PROSTRATE
NARROW LEAVED	BROAD LEAVED	NARROW LEAVED	BROAD LEAVED	

Types of leaves

I - Glossy - yellow green leaves with shining appearance

A. Erect - leaves erect

- Narrow leaved: Leaves are narrow, leathery lanceolate, and erect with pointed tip. The last expanded leaves make an acute angle of about 30° with each other. The leaf margins are straight.
- Broad leaves: Leaves are broad, upper ones erect. The first leaf is lanceolate with acute tip and a pseudostem stout. The last expanded leaf makes an angle of about 45°. The lower leaves are semipendant. Leaf margins appear wavy because of twisting of leaves near the tip.

B. Pendant - leaves drooping

- Narrow leaved: Leaves are narrow, leathery and drooping; the first leaf is narrow with acute tip. Last expanded leaves make an acute angle of about 45°. Margin of leaf lamina straight. Midrib narrow and pale green pseudostem is of medium thickness.
- Broadleaved: Leaves broad, thick coriaceous and drooping lower leaves lanceolate with acute tip. Last expanded leaves make an acute angle of about 45°, leaf margin twisted to give waxy appearance, midrib pale yellow-green in color, pseudostem medium stout.

II. Nonglossy dark green leaves

- Erect: leaves broad, semierect, last expanded leaves make an angle of about 60°, first leaf small, oval with broad tip, leaf margin somewhat wavy due to twisting midrib pale green, narrow but strong, pseudostem stout.
- Pendant: Leaves mediumly broad, drooping, last expanded leaf make an acute angle of about 60°, first leaf is narrow with acute tip, leaf margin gives wavy appearance because of twisting of leaves, midrib narrow, green and weak, pseudostem stout.
- Semiprostrate: Leaves broad and pendant, leaf margin wavy due to twisting pseudostem is not erect medium thin, appearance of tillers during post-rainy season make the plant prostrate in appearance, midrib is narrow weak and green.

GENERAL COMMENTS

From the studies of seedling establishment, we find that there is a wide range of variability of seedling traits in sorghum and also that there is enough scope to select different resistance traits. We need to investigate whether selection of traits for better performance at early seedling stages is related to their performance at later stages. The vigor and productivity of the crop may be established as early as the seedling stage. Leaf growth was found to correlate with emergence index (Allan *et al.*, 1961).

In sorghum, large seeded cultivars produced vigorous seedlings (Kaufmann and Guitard, 1967) with higher yield potentials (Kaufmann and McFadden, 1967). Similarly, high seed protein has also been found to show increase in seedling vigor in wheat and increased vigor was found to be associated with higher grain yield (Ayers *et al.*, 1976; Ching *et al.* 1977; McFadden, 1963; Ries and Everson, 1963; Welch, 1977). There was small but statistically significant correlation between seedling and adult plant characteristics in Russian wild grass. This indicated that the selection in the seedling stage could also have some benefit in breeding for higher yields. It has been possible to release improved cultivars based on selection for improved seedling emergence and vigor from deep planting (Lawrence, 1967). This present study indicates that seed size and seed quality depend on environmental and cultural conditions in which the cultivars are grown. This needs to be taken into consideration in seed production program.

Sorghum genotypes showed a wide range of variability to different seedling resistance traits, emergence from depth of planting and through soil crust, tolerance to high soil surface temperature, soil moisture, and expression of seedling vigor, etc. The relationship between seedling resistance and adult resistance could be correlated. Genetic variability in biochemical traits (eg. chlorophyll, carbohydrate, HCN and wax content) are found to be related to drought resistance. Research in this directions needs to be strengthened for genetic improvement of sorghum for drought resistance.

With the help of some simple techniques mentioned, sorghum genotypes can be identified for different resistance traits. For a long time, physiologists and breeders have been working together looking for a simple resistance trait for incorporation in the breeding material. Identification of a simple seedling trait like glossy and its relation to various resistances have been reported. Incorporation of this trait into sorghum cultivar may contribute substantially to the crop improvement program.

APPENDIX:

TECHNIQUES TO EVALUATE DIFFERENT CROP ESTABLISHMENT TRAITS

At ICRISAT, crop establishment research was intended to study different physical and biotic factors affecting the crop at different stages of development and to develop techniques for identifying resistance sources. Some techniques developed at ICRISAT for the identification of different crop establishment traits are enumerated below and attempts were made to find out genotypic variability for different resistant traits.

1. Seed viability: The objective is to screen the germplasm for seed viability following wetting and drying conditions. This is a potential characteristic in an area where dry sowing is recommended.

Methodology: The seeds are kept in petridishes lined with moist paper for 40-48 hours and allowed to germinate. The germinated seeds are dried at 35 - 40°C in an incubator for two days and then kept at room temperature up to 40 days. Seeds are counted and sown in wooden flats filled with soil or in the field. Final emergence count is taken and expressed as percentage of seeds sown. Genotypes showing good emergence are recommended for dry sowing adaptation.

2. Preharvest sprouting (germinability): Sorghum grains attain germinability at an early stage of grain development. Preharvest sprouting is one of the major problems in early sorghums in rainy season. Lines showing no germinability during and after maturation could aid in reducing grain weathering and improving crop quality. This was done to screen lines showing no germinability during maturation.

Methodology: Grain samples are collected at 5 day intervals from anthesis (50% flowering), pretreated with 0.2% mercuric chloride to prevent mold infestation and tested for germination.

3. Grain mold and grain weathering: Grain mold is a serious problem in sorghum during the rainy season and infestation starts at an early stage of grain development. This again is associated with the problem of preharvest sprouting, thus causing grain weathering and loss of seed viability. This technique is used to screen lines with insignificant mold infestation in the laboratory.

Methodology: Grains are collected at intervals of 5 days from the days after anthesis. One set of grains are put for germination after pretreatment with mercuric chloride for 4 days. Counts of molded grain are made and scores given for mold severity on a 1 - 5 scale (1 = no mold, 5 = severe mold). Sorghum genotypes are shown to exhibit genotypic variability in seedling emergence and seedling vigor of affected with grain mold (Maiti and Banerjee, unpublished).

4. Depth of sowing: The objective is to screen lines showing ability to emerge from deeper depth of planting and with long mesocotyls.

Methodology: screening is done in wooden boxes 160 x 110 x 30 cm. Lines are sown in each box in single row plots on a layer of soil and the boxes are irrigated. The percentage emergence of the genotypes is counted. The seedlings of each line are carefully excavated by slicing vertically parallel to the rows with

a thin metal sheet. The mesocotyl of each seedling is measured and the mesocotyl length computed for each line. Sorghum genotypes can also be evaluated and selected for their ability to emerge from 10 - 15 cm depth by planting in polyethylene bags filled with soil. Genetic variability is found to occur among sorghum in their capability to emerge from deep planting which is associated with mesocotyl elongation (Maiti and Carrillo, 1991). A large number of sorghum lines could be evaluated for their capacity to emerge from deeper depth of planting. Lines selected could be further tested for resistance to other stress factors (Carrillo, 1986).

5. **Effect of soil temperature on sorghum emergence:** This technique is used to study seedling emergence in a wide range of soil temperatures. High soil surface temperature is one of the reasons for poor seedling emergence.

Methodology: brick containers 70 x 160 cm, some 22 cm high are constructed on level ground. They are filled with equal volumes of alfisol. The soil is separated from the brick by PVC film to minimize edge moisture effects. A plastic sheet lies directly on the ground below, thus allowing ready and even drainage to field capacity after watering. Water (40 mm) is applied with a garden sprayer. When the soil reaches field capacity, the lines to be tested are sown. Two lines can be fitted into each container across the length in one row plots. Seeds are sown at a depth of 50 mm. Metal sheets with sharp edges are used as sowing implements to slice through the soil to the correct depth. The soil surface is then levelled and pressed lightly with a sheet of plexiglass to provide a suitable base for the surface treatments. Thermocouples are inserted at depths at which soil temperature is to be recorded. Four thermal regimes can be obtained by the following surface treatments (i) fine charcoal dust (125 g/m²), (ii) bare soil, (iii) light kaolin (125 g/m²) and (iv) heavy kaolin (500 g/m²). The black charcoal absorbs light and increases soil temperature, whereas white kaolin reflects light from the soil surface and maintains a lower temperature compared with that of charcoal treatment. Soil temperature is recorded daily by connecting the lead wire to a multichannelled electronic thermometer. Soil moisture is measured at 0 - 5 cm and 5 - 10 cm depths by the gravimetric method. Emergence counts are made daily until no further emergence occurs. As emergence is influenced by the initial germinability of the seeds, a laboratory germination test is carried out. Emergence is expressed as a percentage of seeds sown and adjusted for germination percentage.

6. **Emergence through soil crust:** Soil crusting is an important problem causing poor seedling emergence in SAT areas. The objective is to screen sorghum lines for emergence ability through crust. Techniques were developed both in the field and brick containers for screening genotypes for emergence ability through simulated crust.

Methodology: depending upon the nature of the soil, 2 techniques can be experimented with in the field:

- a) For fine loamy, calcareous, mixed carbothids, typic, thermic (USDA soil taxonomy) the field is irrigated to excess several days before sowing. It is then levelled by a tractor-mounted leveller. Seeds are sown, one seed per hill at 4 cm depth with the help of a wooden seed dibbler. After sowing, the crust

is induced by uniform application of 6 mm control (uncrusted) plots.

- b) For fine, clayey mixed hyperthermic udic Rodhustalf, the alfisol is ploughed to a fine till with a rotator and then levelled carefully. The seeds are sown at 4 cm depth and 40 mm perfospray irrigation applied. If a gradient in irrigation along the length of the perfos exists, the replications should be laid at right angles to the sprayers. The distance between the two perfos is maintained at 3.5 m by shifting the pipes for the second half of the irrigation time. A light roller is run over one set of plots and unrolled plots from the control. This technique gives opportunity for testing genotypes for emergence through soil crust and compaction.

- c) For brick flats = brick flats similar to those used in the soil temperature studies. They are filled with equal volumes of the fine alfisol. Water 40 mm is applied and the soil allowed to come to field capacity. Seeds are then sown at 40 mm depth using metal sheets with sharp edges to slice through the soil to the correct depth. About four hours after sowing, 60 mm water are sprinkled from 1 m above, which helps in the lateral migration and accumulation of fine particles to form a crust.

In all these techniques, crust strength, soil temperature and moisture are monitored daily. Emergence counts are made each day.

Drought resistance at the seedling stage: Techniques exist for field and semi-controlled conditions (in brick containers and PVC cylinders in a greenhouse). In both, limited water (40 mm) is applied after sowing, without further watering. As seedlings grow in the declining soil moisture, they slowly come under stress and began to wilt. Visual scores for wilting were given on a 5-point scale. Stress is released when most of the lines show wilting and some lines have no chance of recovery. Recovery scores on a 5-point scale (1 = best recovered, 5 = least recovered) and percentage survivals are noted. Soil moisture is monitored at different depths periodically. Individual details in each technique are dealt with below.

Methodology: sorghum lines are flat planted in an augmented random block design (RBD) with 2 checks entries repeated in each block. Controlled perfospray irrigation is given after planting. If a gradient in irrigation along the length of 'perfos' exists, the replications should be laid at right angles to the sprayers. Irrigation differences may result in high CVs. Brick containers similar to those used in the soil temperature studies can be employed and an augmented RBD used. Each flat has 20 plots, of which 16 are for test entries and 4 reserved for 2 checks which should be repeated twice in each container. There are 15 plants in each row. Portable rainout shelters can be used to protect the brick containers from rain. Container effects can be estimated as a difference between the mean of the checks within a container and their overall mean. The test entries are adjusted for the container effects. The adjusted values are then analyzed to assess for resistance or susceptibility of the test entries.

Intervarietal competition exists in the brick containers, therefore, the genotypes can be sown separately in sealed PVC cylinders (30 cm length with an internal diameter of 10 cm) filled with equal weights (4.4 kg) of alfisol. Measured amount of water (approx. 40 mm) are applied equally to each cylinder. The

amount of water is determined from preliminary trails to get the required amount of water to avoid wilting symptoms at the seedling stage. The plants are thinned to 6 per meter square day after emergence. Root growth is restricted. To prevent the sidewall of the cylinder from getting heated, it could be coated with white paint.

8. **Technique for seedling drought resistance in hydroponics:** The screening for seedling drought resistance is generally done in soil of flats, pots or beds in a greenhouse or growth chamber. When the seedlings are established, water is simply withheld until they show severe wilting. At this stage, stress is released by watering and survival counts taken. The problem with this method is that it is very difficult to control the level of stress to which the plants are exposed, particularly with repeatability of subsequent experiments, and water extraction may differ markedly in the vicinity of individual plant roots. The technique adopted by Sullivan and Ross (1979) overcomes these defects.

Methodology: seedlings are grown hydroponically in rows of plastic dishes. The seeds are first germinated in wet paper towels and then transferred to the dishes or 3 days to the dish pans. An acrylic plastic tray is cut to fit the pans. Rows of holes (about 2 mm diameter) are drilled and spaced about 2 cm, with 4 cm between rows. A countersink is made above each hole. The tray is placed in the hole when the seedling is transplanted with the seed being in the countersink area. The solutions need to be aerated for growth of sorghum seedlings. When the seedlings are 7 to ten days old, Carbowax 60 is added to the solutions in increments over a 3 day period until a stress of 15 bars is reached. The plants are then evaluated for drought resistance by exposure to the stress for several days. For a small number of entries, the height, leaf number, leaf area, maximum root length and dry weight are measured and compared to nonstressed controls. When many genotypes are evaluated, they are visually ranked from 1 - 5. One is assigned to green, two to plants with few, or no symptoms of drought injury. A rating of 5 is given to dead plants.

9. **Visual scoring of seedling vigor:** The objective of this technique is to estimate rapidly and efficiently the seedling vigor of a large number of lines. The visual scoring system used is a relative one, based on the range of variability in seedling size in the material being scored. The individual 15 ratings (1 = most vigorous, 5 = the least vigorous) are based on individual plots within an experiment which serves as a reference for scoring all entries. The following factors enter into the assessment of seedling size: height, pseudostem thickness, spread of leaf canopy and/or the length of breadth of the individual leaves. The restriction to a limited number of classes may be a limitation to the use of visual scoring for some types of studies (e.g. parentprogeny comparisons).



LEAF AND STEM

LEAF MORPHOLOGY

Each sorghum leaf consists of a thin flat lamina with a definite midrib and a thicker rigid leaf sheath claspings the pseudostem internode. The midrib may be strong or weak, white or green in color. Leaves may be erect, semi-erect to drooping; the leaf blade and sheath meet at a point called collar at different angles to the stem which may vary from almost vertical to near horizontal. At the base of the lamina ligules project from the leaf base. Leaf length becomes gradually shorter and smaller towards the tip. The terminal leaf is called flag leaf. The length of leaf may be as long as 1 m and the width 10 to 15 cm. The number of leaves in well adapted genotypes vary from 14 to 17, whereas in less adapted ones there may be as many as 30 leaves. The leaves are arranged in 2 ranks alternatively at an angle along the stem and each node. The sheath is attached to the node, and surrounds the internode, and often the node above it. In some cultivars the leaf sheath is covered with a waxy bloom. Leaves are glabrous except on the inside, just above the membranous ligule and on the cuticle near the junction with the sheath. The leaf margins are smooth or scabrid (Fig. 4.1; House, 1980).

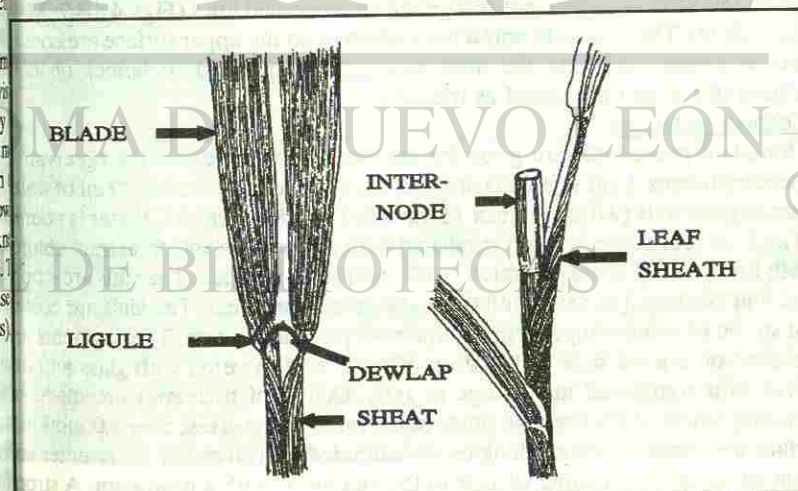


Figure 4.1 Morphology of a leaf showing its parts and its attachment with stem. a) A portion of a leaf; b) Attachment of leaf sheath with stem.

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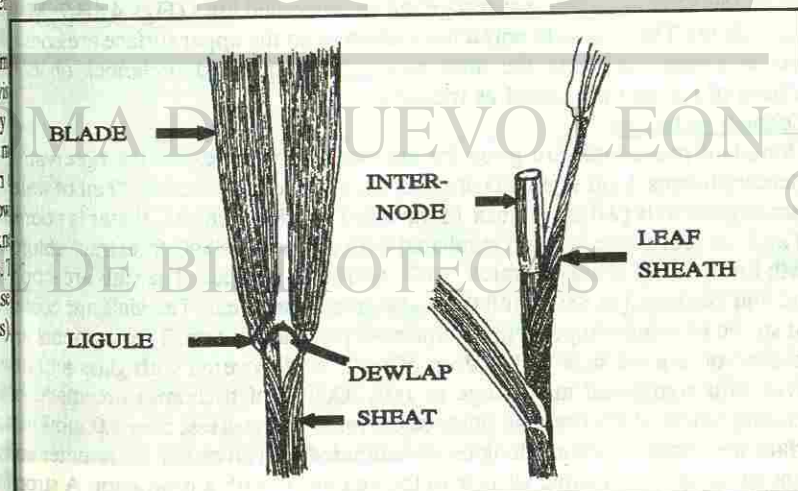


Figure 4.1 Morphology of a leaf showing its parts and its attachment with stem. a) A portion of a leaf; b) Attachment of leaf sheath with stem.

LEAF ANATOMY

The development of sorghum is typical of grass leaves described by Dale (1957). It begins development as a single ridge which is oriented laterally on the meristem. The crescent-shaped primordium grows into a hood-shaped structure which envelopes the apical dome.

Leaf surface

Leaf epidermal cells are of various sizes with wavy outline and stomata between 2 adjacent stomates (Fig. 4.2). After a 30 hr treatment with cold temperature (10°C) one third of the upper mesophyll were badly swollen while in the rest, chloroplast contraction and reduction in starch grain size occurred. This affected the pattern of photosynthetic radiocarbon exchange (Brooking and Taylor 1977).

Preliminary studies by Yadav (1976) indicate that in lines resistant to pest fungus, the leaves have a thickened cuticle and hypodermis in the midrib. Epidermal pattern showed higher number of stomata with shorter length and wider guard cells in resistant forms.

The epidermis of leaves of many of the glossy lines (85%) show the presence of microscopic hairs called trichomes. Trichomes are single-celled projections, easily visible at 160x magnification on the epidermis of the leaf. They are often pointed at the tip. The size and morphology of the trichomes vary in different genotypes (Plate 4.1; Fig. 4.2), and they are directed towards the leaf base, more being present on the upper (adaxial) surface (Tables 4.1-4.2).

Trichomes are dense at the tip, intermediate at midportion, and less at the base of the leaf (Fig. 4.3). It is difficult to distinguish genotypes on the basis of trichome density as some trichomes are not visible under a low-power (X160) microscope. Their length varies from 20 to 55 μm and these glandular trichomes can be observed under a high-power microscope or a scanning electron microscope (SEM). These trichomes are bicellular and have a rounded tip. Lines with typical trichomes on the abaxial surface are recognised as trichomed lines (Figs. 4.4-4.7; Maiti *et al.*, 1980b). The lines with only a few trichomes on the upper surface are considered as trichomeless and the lines with typically pointed trichomes on both surfaces of the leaf are called as trichomed lines.

Trichome technique

Standard procedures are given for the clearing of leaves for the observation of leaf trichomes. Leaf segments of about 1-2 cm^2 are incubated in 20 ml of water in small glass vials (2.0 cm diam. x 7.5 cm high) for 15 min./85°C. Water is poured off and the leaf tissue is again incubated with alcohol at 85°C to extract chlorophyll; finally 20 ml of concentrated (90%) lactic acid is added. The vials are shaken and incubated at 85°C until the leaf segments are clear. The vials are cooled and stored at room temperature for microscopic examination. The segments are mounted on a glass slide with a drop of lactic acid, covered with glass and observed in a compound microscope at 160x. Counts of trichomes are made in randomly selected microscopic fields of 0.8 mm^2 and expressed on 1.0 mm^2 surface area basis. Trichome lengths are estimated with an ocular micrometer and trichome angle is estimated visually to the nearest 5° with a protractor. A strong relationship between trichomes on the lower surface and shootfly resistance has been found (Maiti and Bidinger, 1979).

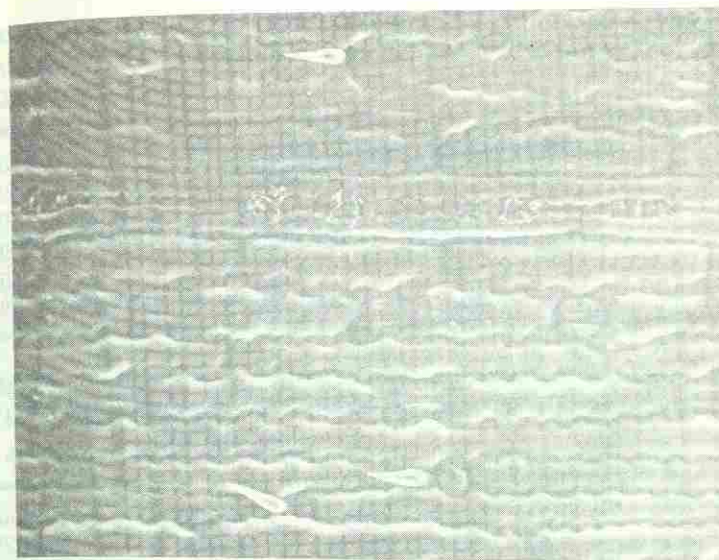


Figure 4.2 Leaf surface of IS 4664 showing morphology of epidermal cells and attachment of trichomes, under the light microscope.

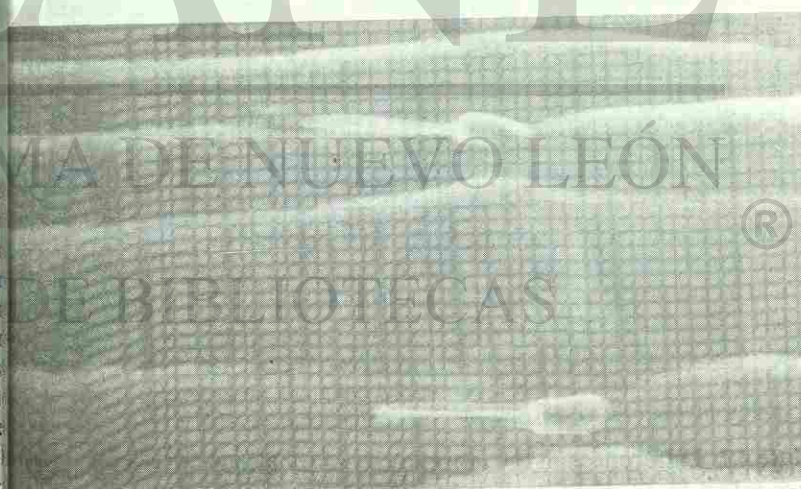


Figure 4.3 Scanning electron micrograph of the surface of a leaf of IS-844, showing glandular bicellular trichomes.



Plate 4.1 Differences in the morphology of trichomes of sorghum. Drawings taken from microscope transparencies of the abaxial surface of leaves.

Table 4.1 Trichome density (mm^2) on the center portion of the adaxial and abaxial surfaces of the fifth leaf. Means are of 10 leaves per cultivar and 2 microscope fields per leaf.

Genotype	Adaxial surface	Abaxial surface
IS 1054	17 ± 1.3	6 ± 1.0
IS 2146	45 ± 3.8	27 ± 4.4
IS 2314	22 ± 1.6	4 ± 0.6
IS 5604	28 ± 1.6	9 ± 2.2
IS 5484	37 ± 5.1	22 ± 4.1

Table 4.2 Range of trichome density on the abaxial leaf surface of the fifth leaf in selected sorghum cultivars. Means are of 10 leaves per cultivar and 2 microscope fields per leaf.

Genotype	Trichomes / mm^2	Genotype	Trichomes / mm^2
IS 1119	46 ± 4.9	IS 5613	45 ± 4.7
EN 3342-4	45 ± 4.1	IS 2146	45 ± 4.4
IS 2205	30 ± 4.1	IS 18588	28 ± 2.5
IS 5622	28 ± 4.4	IS 1054	8 ± 0.9
NCL-3	4 ± 1.3	IS 5067	4 ± 0.9

Electron microscopy of glossy and nonglossy lines (Maiti *et al.*, 1983b)

For the SEM of the leaves of glossy and nonglossy lines, a JOEL SEM was operated at 18 kv with magnification 1100X and 16 kv at magnification 15000X, 100X. The lower surface of each cultivar was photographed at 200X, 1500X and 1000X. Silica deposits, trichomes and epicuticular wax were the main features of sorghum leaf surface.

Silica: Dumbbellshaped deposits, with either 2 or 3 bumps are regularly spaced along the veins. Along major veins, sometimes 2 or 3 rows of silica bodies are also present (Fig. 4.4-4.5). All cultivars show the presence of these lines of silica, irrespective of their glossy or nonglossy nature.

Trichomes: All sorghum genotypes show trichomes under SEM. Two types are observed, prickly hairs and microhairs. Prickly hair have pointed tips and are nonglandular, but micro hair is bicellular and looks glandular (Fig. 4.6-4.7). In a few cases, both types of hair are present (e.g., cultivars Swarna and IS 4405). The majority of glossy lines have prickly hair. The density of hair varies between cultivars and the distribution along the leaf is very irregular. Shape, size and the orientation to leaf surface of pricklyhair is variable with hair of different morphologies occurring together.

Wax: Protruded wax filaments on sorghum leaves were reported by Sánchez-Díaz *et al.* (1972). Clusters of filaments were more scattered further away from the midrib on leaf and groups of 2 to 5 filaments occurred at random between the larger clusters. The wax filaments reflect some radiation, lowering the net radiation



Figure 4.4 SEM of the surface of a leaf showing bilobed and trilobed silica crystals.

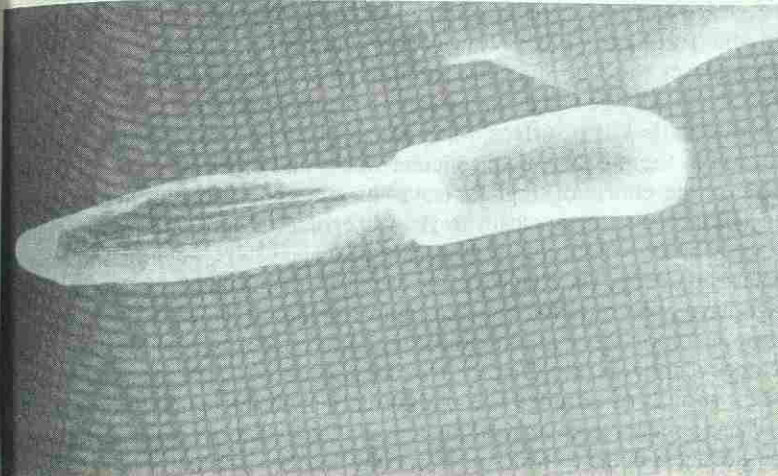


Figure 4.6 SEM of the surface of a leaf of IS-4846, showing a view of a multicellular trichome.



Figure 4.5 SEM of the surface of a leaf showing trilobed silica crystals.

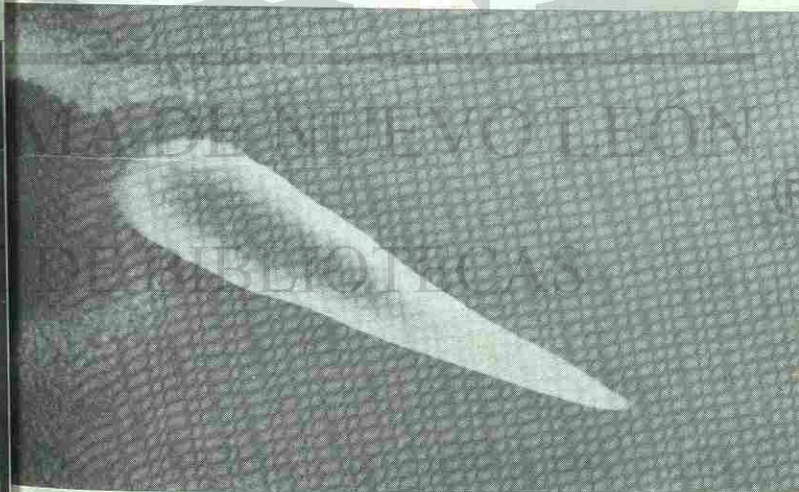


Figure 4.7 SEM of the surface of a leaf of IS-4777, showing an augmented view of a pointed trichome.

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and will thicken the boundary layer next to the leaf, thereby increasing resistance to diffusion of water, oxygen and carbon dioxide in and out of the leaf (Haberlandt, 1928).

The glossy leaf character in sorghum was described by Maiti and Bidinger (1979) and Tarumoto (1980). The ultrastructure of the surfaces of glossy and nonglossy leaves were examined by Tarumoto *et al.* (1981) and Maiti (1986) with the help of a SEM. The nonglossy lines showed high density of starshaped epicuticular waxes on their leaf surface, whereas the glossy lines were characterized by a reduction in the number of epicuticular waxes and different shapes of waxes.

Waxes of the cuticle of sorghum leaves have been extracted with chloroform and analyzed chromatographically by Bianchi *et al.* (1977). The classes of organic compounds which constituted wax were n-alkanes, esters, aldehydes, alcohols, n-alkenes and sterols. The changes in the chemistry of epicuticular wax of sorghum with age have been reported by Atkins and Hamilton (1982a).

Glossy and nonglossy cultivars can be separated in 2 groups on the basis of the appearance of the wax (see Chapter 3 for details). Between the silica bodies, nonglossy lines show strands of extruded wax of different lengths along the veins (Fig. 4.10). There appears to be no relation between the extent of extrusion of the wax and the glossiness of the cultivar. In glossy cultivars, the smooth wax layer covers the epidermal cells and the cuticle shows patchy aggregations of large, irregularly shaped crystals (Fig. 4.11). The density of these aggregations differs with cultivar but areas of smooth wax are always visible, and silica bodies are rarely covered to any extent by these wax crystals.

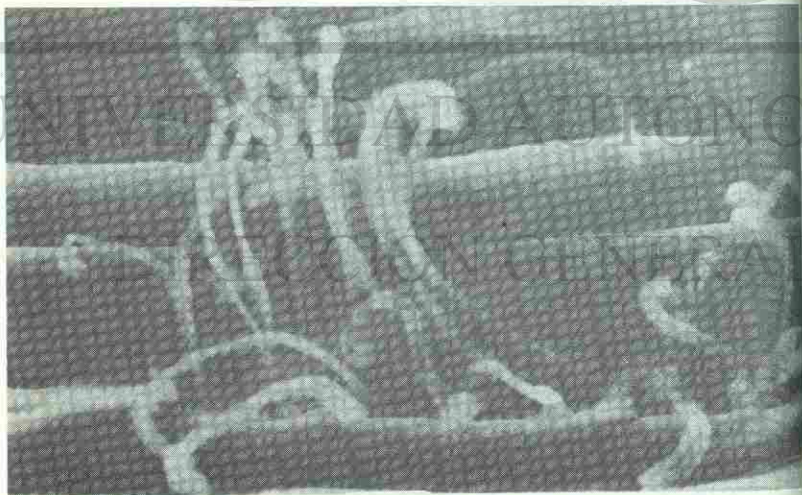


Figure 4.8 SEM of the surface of the surface of a leaf of IS-4776, showing long wax strands.

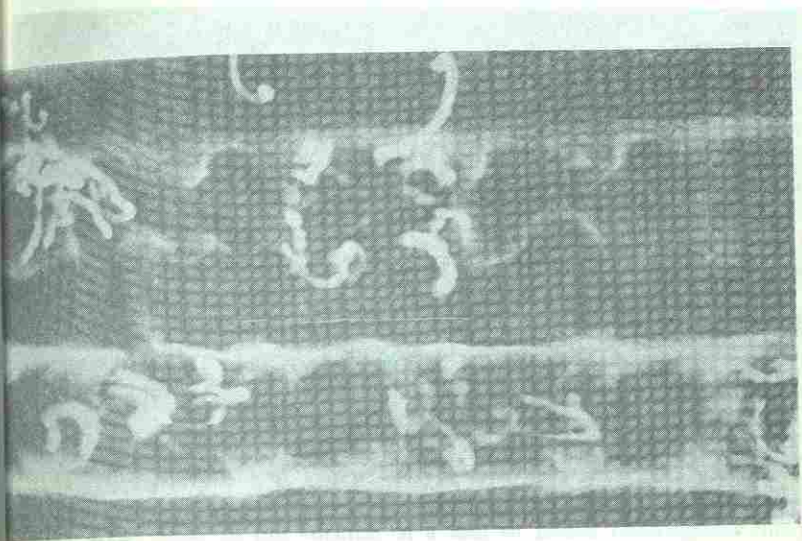


Figure 4.9 SEM of a leaf of IS-4664, showing groups of medium length wax strands partially covering the silica crystals.

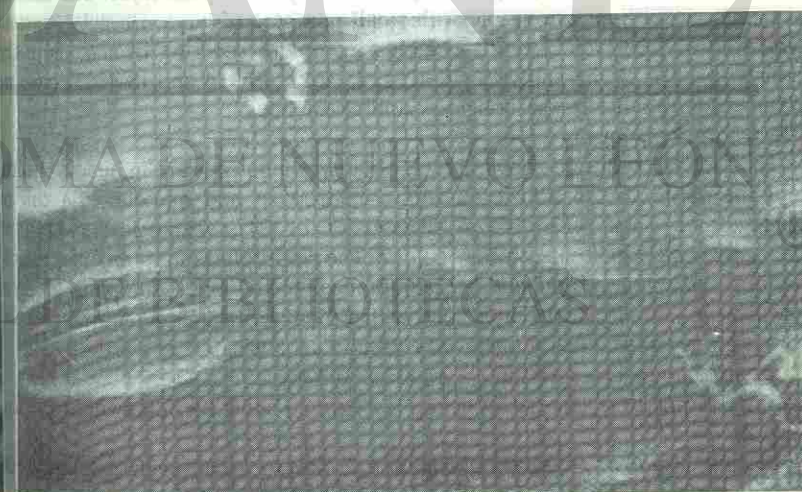


Figure 4.10 SEM of the surface of the surface of a leaf of IS-5031, showing short wax strands.



Figure 4.11 SEM of the surface of the surface of a leaf of IS-2123 (G line), showing a smooth wax layer and a trichome (1500X).

In the nonglossy lines, very little smooth wax is visible on the leaf surface. Uniform needleshaped wax crystals are observed under high magnification (Fig. 4.12). Silica bodies are also generally covered by the crystal layer. The smooth areas on glossy lines are visible with small numbers of large, irregular crystals which is in sharp contrast to the almost complete covering of crystals in nonglossy lines. Some cultivars (IS-4292, IS-4621, IS-914 and IS-4405) have clear characteristics of the nonglossy and glossy lines.

Electron microscopy

Electron micrographs show that the photosynthetic cells are in bundle sheath and the membrane organization within chloroplast and mitochondria can be distinguished (Figs. 4.13-4.15). A crosssection of C4 sorghum leaf shows bundle sheath and mesophyll chloroplasts. The chloroplasts show an outer double-membraned envelope and lamellar membrane in the stroma. Osmophilic granules are profuse. Bundle sheath chloroplast with distinct arrangement of thylakoids and starch granules are clearly observed (Maiti *et al.* 1983b).

Leaf anatomy in crosssection (Maiti *et al.* 1983b)

Lamina: Transverse sections of young leaf lamina show the following structure (Fig. 4.16-4.17):

Epidermis: Epidermis consists of roundish to flattened cells with thin cuticle on both surface of the leaf. Stomata are embedded in a suboptimal cavity with guard cells. Bulliform cells are present on the upper epidermis.

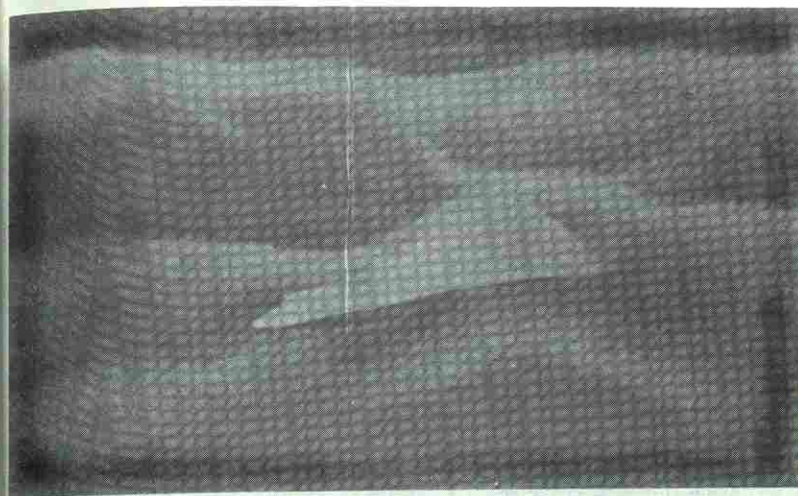


Figure 4.12 SEM of the surface of a leaf of E-202 (Non-glossy line), showing an uneven surface, the underlying needleshaped crystals and a trichome (1500X).

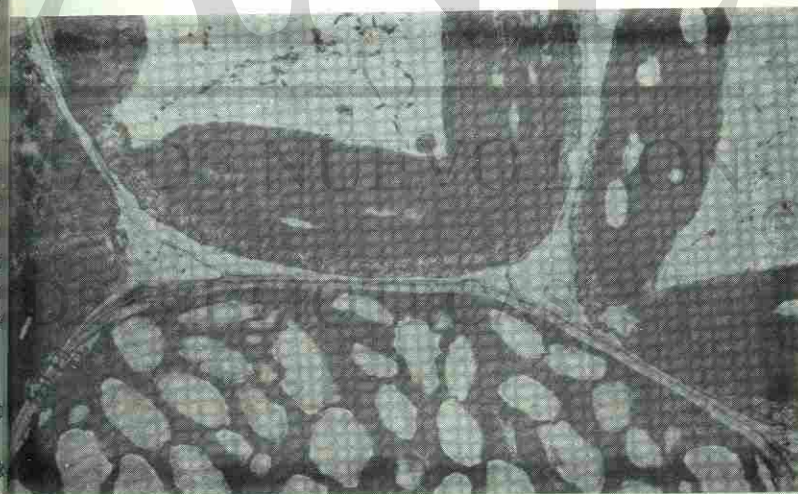


Figure 4.13 Electron micrograph of a sorghum leaf, showing a mesophyll chloroplast (top) and a bundle sheath (bottom, with large starch granules).

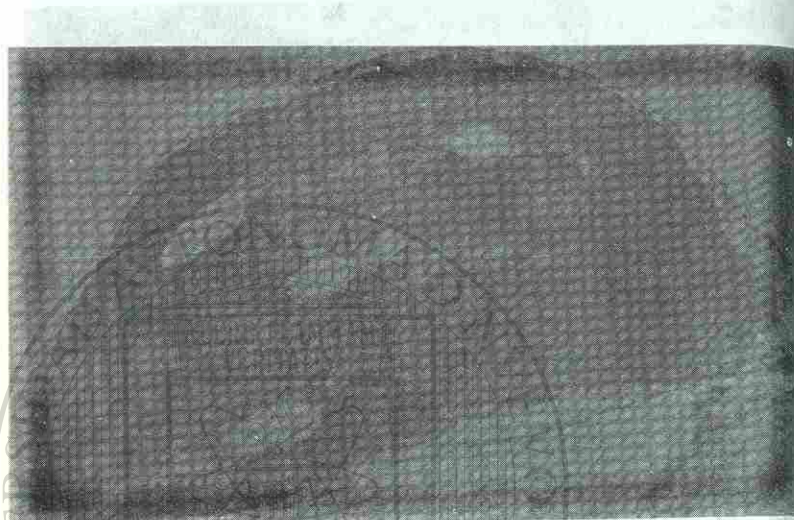


Figure 4.14 Electron micrograph of a mesophyll chloroplast.

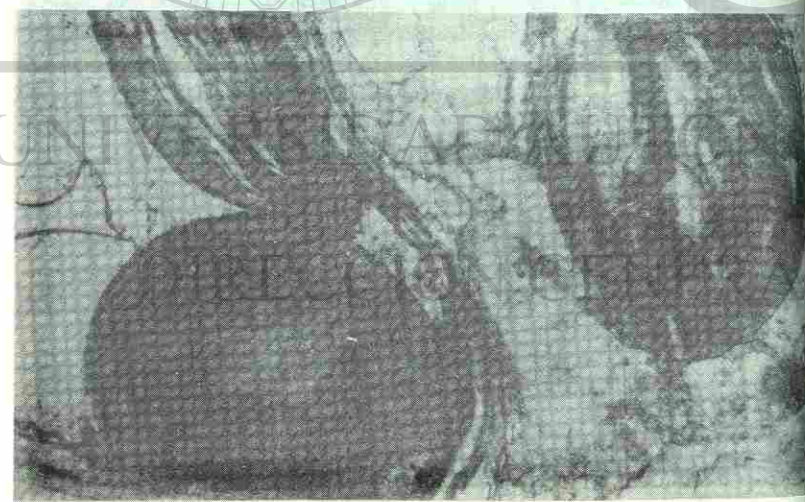


Figure 4.15 Electron micrograph of a section of a leaf, showing differences between a transverse and a longitudinal cut.

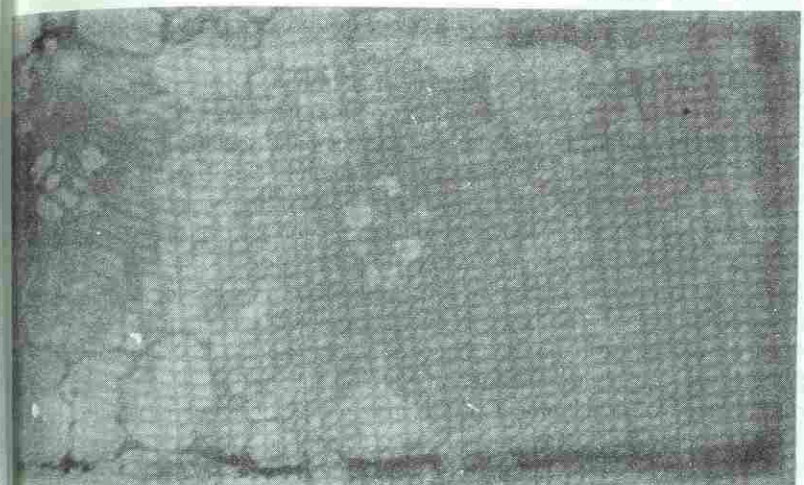


Figure 4.16 Transverse section of a young leaf, showing upper and lower epidermis, sunken stomata (substomatal cavity), mesophyll cells and Kranz tissue.

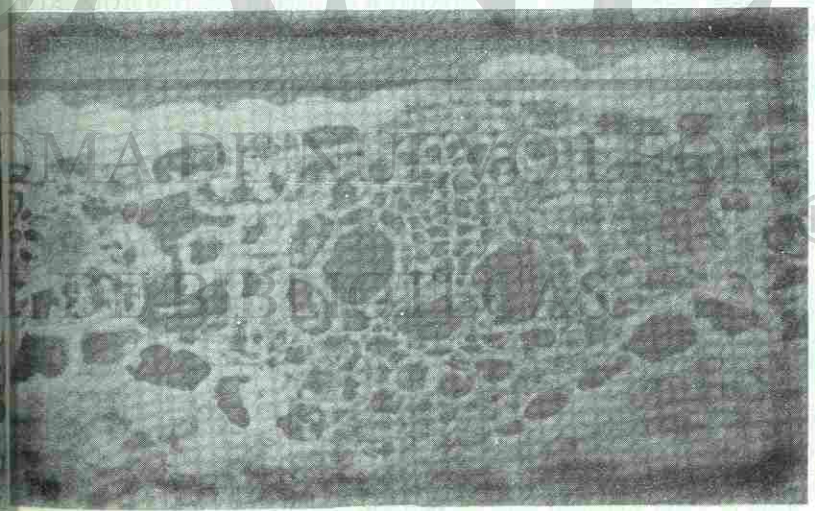


Figure 4.17 Scanning electron micrograph (SEM) of a crosssection of leaf, showing 'Kranz' anatomy.

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Mesophyll: Mesophyll consists of loose parenchymatous cells with profuse intercellular spaces. Mesophyll parenchyma surrounding the vascular bundle has distinct chloroplasts.

Vascular bundle: Young bundle sheath cells shows presence of distinct chloroplasts (Kranz tissue).

Midrib: Midrib shows the presence of small round, epidermal cells on both surfaces of the leaf with more cuticular thickening on the lower surface. Parenchymatous cells are compactly arranged. Large and small vascular bundles are present below the lower epidermis. A large vascular bundle is capped with thick sclerenchyma sheath, followed by 3 small vascular bundles with no-sclerenchyma sheath. Kranz tissue is prominent. Two large metaxylem and 2 small protoxylem vessels are distinct in the large vascular bundle (Fig. 4.18-4.19).

Pseudostem: Transverse section of a pseudostem shows developmental pattern of tissue in leaf sheath. The center of the culm shows crosssection of younger stem in which the tissues are at different stages of development. The sheath surrounding the stem is the youngest developing leaf. Subsequent enveloping leaf sheath show advanced stage of development of the mesophyll cell, epidermis and vascular bundle. The outermost leaf sheath shows well developed epidermal cells, sclerification of the bundle sheath and developed vascular bundle (Fig. 4.20-4.21).

Glossy lines do not show distinct differences from nonglossy in anatomical characteristics, but glossy lines show more cuticular thickness compared to nonglossy ones. Chloroplast containing mesophyll are organized in relation to vascular tissue. Typical Kranz anatomy, characteristic of C₄ (dicarboxylic acid pathway of photosynthesis) plants is observed, and consists of an inner cylinder of bundle sheath cell around the vascular bundle and adjacent layer of mesophyll cells. Two to three rows of mesophyll cells are arranged in concentric circles about the vascular bundles. Kranz tissue structure is also clearly observed in crosssection of midrib.

FACTORS THAT DETERMINE LEAF DEVELOPMENT

Growth of leaf is controlled by different factors. Dale (1982) explained the effect of environmental factors on leaf growth which are summarized here:

Light: chlorophylls a and b control the growth of plants in the presence/absence of light. The duration of light period remaining constant, there is an increase in leaf area with intensity of light. A curvilinear relationship exists between leaf area and photoperiod, light intensity remaining constant. The response of leaf area to the total quantity of light per day is a complex phenomenon.

Temperature: temperature has a marked effect on the initiation of the primary and number of leaves.

Water: growth of cells in leaves is largely dependent on water content which maintains the turgor pressure. Leaf expansion is highly dependent on water uptake. The water content of the leaf is brought about by maintaining a gradient of water potential between the cells and the water source.

Mineral nutrition - Nitrogen, phosphorus, potassium and magnesium are important for leaf growth. Pests affect leaf growth considerably.

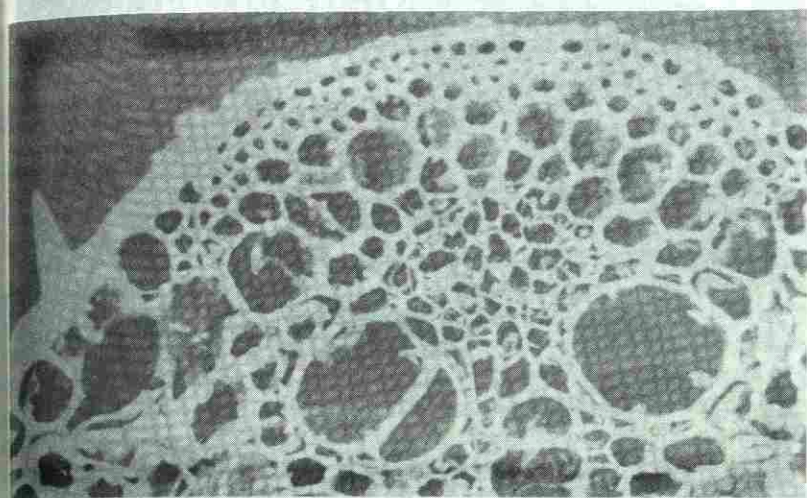


Figure 4.18 SEM of the midrib showing thick walled epidermis (E), trichome (T), sclerenchyma sheath (Scl.) and 'Kranz' anatomy.

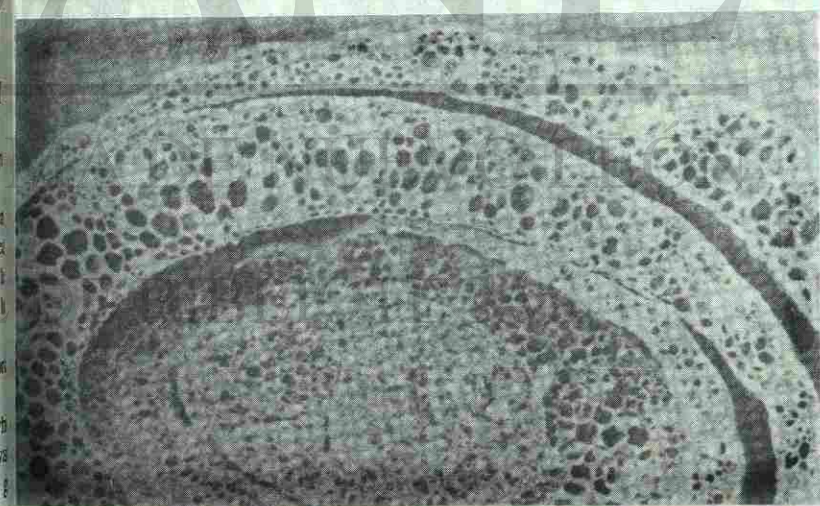


Figure 4.19 Transverse section of a midrib, showing the orientation of the vascular bundle and the internal tissues.

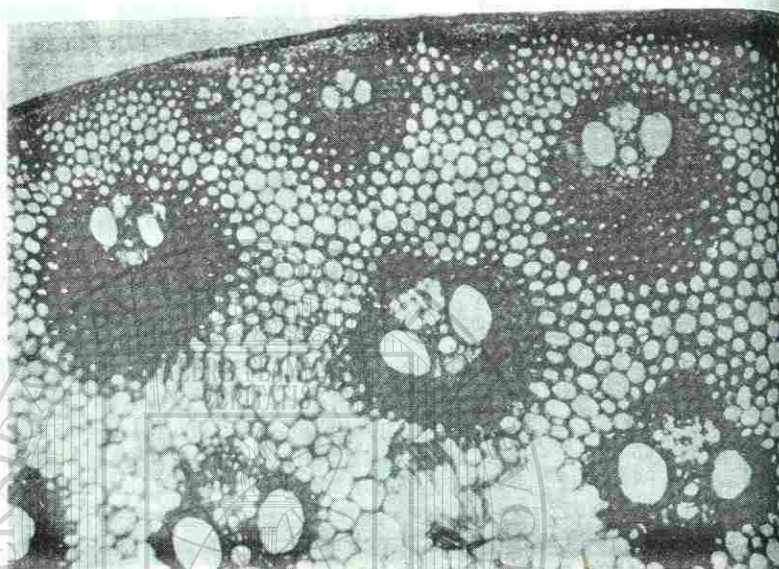


Figure 4.20 SEM through transverse section of a culm, giving orientation and development of the tissue of the leaf sheaths encircling the stem.

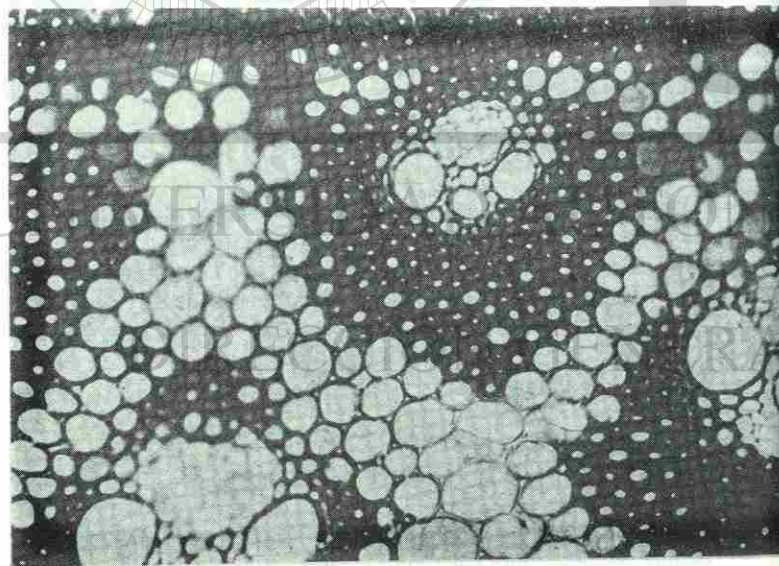


Figure 4.21 Transverse section of a pseudostem, depicting little mechanical tissue and small and large vascular bundles in the peripheral region.

Temperature is by far the major deciding factor in determining the length of each developmental phase and the heat unit requirement for each phase differs in different phenological stages of the plant (Seetharama, 1980).

1. A leaf is said to be visible when the tip of the leaf blade is seen in the whorl.
2. A leaf is considered as expanded (maximum leaf area) when the collar is visible.
3. Leaves need to be counted from the bottom following the development of the plant. The first leaf is usually less rectangular and has a round tip.
4. Culm means the stem along with the leaf sheath around it.

In sorghum 4 - 5 leaf primordia are found in the embryo (inside the kernel itself). The remaining leaf primordia are produced from the apex of the shoot. In cereals, cell division and leaf expansion stop first at the tip when leaf lamina emerge from the encircling leaf sheath that has already stopped growing. Therefore, the growth of the whole leaf lamina is complete with the emergence of ligule but leaf sheath continues to expand (Milthorpe and Moorby, 1972). The leaf meristem is present at the base of the leaf enclosed in the whorl of the centre of pseudostem and the leaf cells are produced by cell division. The leaves are expanded by cell elongation at the base of the leaf. This helps in the extension and final expansion of the leaves. Each leaf passes through 3 stages of development: initiation, expansion and senescence. The leaf growth and canopy development of the crops are of great interest to crop physiologists as these factors contribute to the photosynthesis and yield of crop. Large differences are found to exist in leaf growth and canopy development in different sorghum cultivars.

Leaves grow through 3 main phases of development: emergence, expansion and leaf area development.

Leaf emergence

Clark (1970) studied from both longitudinal and transverse sections, the number of embryonic leaves of some cultivars of sorghum, sudangrass (*Sorghum sudanense*), Johnsongrass (*S. halepense*) and shattercane. He reported 4 embryonic leaves in *S. bicolor* and shattercane but 3 embryonic leaves in Johnsongrass and sweet sudangrass.

In general, 6 or 7 embryonic leaves emerge at approximately 0.5 leaf per day; the rate of emergence of the subsequent leaves is slower. The rate of emergence and the final number of leaves vary in different cultivars, with early maturing cultivars generally having fewer leaves and a faster rate of emergence. The rate of development of the total leaf area per plant is a product of the rate of leaf expansion, size and the longevity of individual leaves.

The rate of leaf development is obtained by counting all the leaves at constant intervals on the stem from base to the top of the plant. The rate based on leaves emerging from enclosing leaf sheath is usually lower than that based on the portion of leaf primordia at the base of the culm. At panicle initiation, all the leaf primordia are developed by the shoot meristem and enclose the reproductive apex, but only 7 to 9 leaves would have expanded by that time. The rate of leaf emergence increases with a rise in temperature (Wade *et al.* 1982; Peacock, 1982). Leaves elongate quickly after emergence and start functioning. The life span of individual leaves differs widely among cultivars.

A study during rainy season with a number of cultivars in 1981 at ICRISAT the author showed that it took about 5 days after seedling emergence for the first leaf to emerge and 10-12 days for the fifth leaf. It took about 25-30 days for the expansion of 6 to 7 leaves by which time the vegetative shoot apex was converted into a reproductive meristem. By this time all the leaf initials were laid down. Subsequent leaves expanded slowly with elongation of stem internodes. It took about 35-50 days for the final leaf to emerge (flag leaf) depending on cultivars (unpublished).

Leaf extension

Wade *et al.* (1980) laid emphasis on techniques to study the effect of temperature on leaf extension rate, since it is a direct function of the total leaf expansion process and is also the most sensitive of all components of leaf development.

Leaf extension rate is equal to the change in leaf length divided by the time interval between the leaf length measurements. Leaf length is measured with a ruler as the distance from the soil surface to the tip of the expanding leaf. However, during the growth stage when panicle development culminates in anthesis the increase in leaf length will consist of stem extension plus leaf extension. So the extension rate is equal to the change in ligule height divided by the time interval between ligule height measurements. The true leaf extension rate is then determined by subtracting the stem extension rate from the original leaf extension rate. Ligule height is measured with a ruler as the distance from the soil surface to the ligule of the youngest fully expanded leaf. These measurements are normally made twice a day, at 9:00 and 16:00 hours, throughout the expansion of the leaf. The leaf extension rate (LER) could be calculated in the following way:

$$\text{Leaf extension rate (LER)} = \frac{(LD2 - LD1)/(D2 - D1) \text{ [mm/hour, cm/day]}}{\text{(Total change in leaf length) / (Time)}}$$

where: LD1 = leaf length at day 1 (D1), LD2 = leaf length at day 2 (D2)

Temperature can be measured with thermistors connected to a recorder, and appropriate temperature for each leaf being that measured at the height of the growing point. Leaf extension rate is then plotted against temperature and a regression of leaf extension rate on temperature is calculated. In comparing genotypes, treatments, slope (responsiveness), maximum rate and critical temperature at which leaf extension reaches its limit are important in interpretation of the data (Wade *et al.*, 1982). However, since the leaf extension rate (LER) is just one component of leaf area development, it is essential to simultaneously study other components affecting the process, viz. lifecycle duration, the timing of panicle initiation and its influence on leaf number, the rates of leaf appearance, leaf expansion and leaf senescence, duration of leaf expansion, and finally, the combined effects of these factors on leaf size, leaf area index and leaf area duration.

Leaf elongation of sorghum is slowest at night, presumably because of low temperature, but reaches a peak in daytime, when leaf water potential (Ψ) is high. Solute potential also decreased during daytime which maintained the turgor pressure necessary for cell expansion (Acevedo *et al.*, 1979). Peacock (1979) reported a correlation between temperature, leaf extension and expansion in sorghum.

The effect of fertility level (N) and water on leaf extensions of cultivars was

studied by Seetharama *et al.* (1982) during 1981 post-rainy season, in vertisols at ICRISAT. The authors observed that LER was a direct function of temperature in the range of 10 to 30°C. LER is known to have a curvilinear response to temperature (Fig. 4.22). This study also points out that LER was affected more by nitrogen stress than by water stress. The duration of extension was unchanged under water stress but time of emergence, full expansion and longevity of leaves under different irrigation treatments were affected; at the same time, individual leaves of zero N plants took 13 (leaf 4) to 20 (leaf 14) more days to emerge than those under 80 kg N/ha.

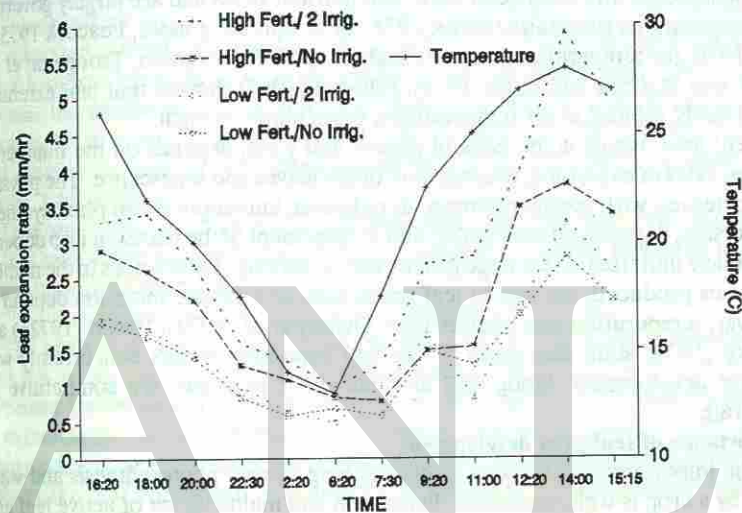


Figure 4.22 Diurnal variation in leaf expansion rates in sorghum under different watering (2x) and fertilization (80 kg N/ha) treatments.

Wade (1980) stated that the maximum area of each leaf is a product of duration of leaf expansion, LER and leaf width. He also stated that the combined effect of area per leaf and number of green leaves determines maximum leaf area, which was reduced drastically under nitrogen stress but less so under water stress from 40 days after sowing.

There are few reports about the effect of low temperature on leaves. McWilliam (1983) stated that high temperature accelerates leaf growth and low temperature intensifies injury in chilling sensitive tissue. Slack *et al.* (1974) observed chlorotic bands on sorghum leaves exposed to temperatures close to 0°C. McWilliam *et al.* (1979) concluded from electron micrograph studies that the failure to develop chloroplasts under low temperature is associated with the arrested development of thylakoid membrane system of the developing plastids.

Downes (1968) showed that leaf appearance in sorghum increased linearly with air temperature from 13 to 23°C. Genetic variation in leaf growth in relation to

temperature was large (Quinby *et al.*, 1973); Wade, unpublished). Research ICRISAT (Peacock, 1982) has shown that the rate of leaf extension is markedly reduced above 34°C. The base temperature for high leaf extension is around 15.5°C. Water stress and high temperature had a drastic effect on the rate of extension.

Peacock (1982) reviewed the effect of environment on leaf growth. McCree and Davis (1974) reported that dry matter production is highly affected by leaf area, especially during Growth Stage 1 (GS1), when the canopy is developing. In Poaceae, the components affecting leaf area development are time for panicle initiations (through its leaf number), rate of leaf appearance, leaf expansion and leaf senescence, the absence of water and nutrient stress and are largely governed by temperatures (for maize, Watts, 1974; for temperate grasses, Peacock 1973 and 1976; for temperate cereals, Gallagher, 1979; for sorghum, Troughton *et al.*, 1974, and McCree and Davis, 1974). Johnson (1967) showed that leaf extension was closely related to air temperatures, particularly at night.

Leaf area, which is the basis of growth and yield, depends on the number of leaves, rates of expansion, eventual size of the leaves and senescence. The physiology of leaves, with special reference to radiation, interception and photosynthesis conversion, depends on the number and arrangement of the leaves; it also depends on panicle initiation where large genetic variations exist. Differences in the number of leaves produced, the rate of leaf production and panicle initiation depend on cultivar, temperature and photoperiod (Quinby *et al.*, 1973). Eastin (1972a) and Brown (1978) state that much of the leaf expansion occurs concurrently with panicle development during GS2 and that the 2 processes are competitive on the substrate.

Importance of leaf area development

The importance of leaf area in determining canopy photosynthesis and water used by a crop is well recognized. Formation and maintenance of active leaf area is essential for continued production of photosynthate to maintain carbon and energy flow to both developing grain and plant tissues (Jordan *et al.*, 1980). Measurement of the light photosynthetically active radiation (PAR at 400-700 nm wavelength intercepted by the crop canopy) has become a very useful tool in such studies. The net PAR for a plant can be determined once the total canopy leaf area of the plant affecting leaf area development is calculated (Chapter 1).

The information on leaf area is needed for calculating transpiration when the plant canopy provides only a partial ground cover. In the dynamic sorghum model of Arkin *et al.* (1976), the leaf area development was modelled from inputs of number of leaves produced by the hybrids plants and the maximum area of each leaf. The rate of leaf expansion out of the whorl was related to the mean diurnal temperature when the plants were adequately watered. Arkin *et al.* (1976) developed a mathematical model for computing light interception in a grain sorghum plant canopy. Sound data base between measured and computed dry matter accumulation in the study by Arkin *et al.* (1976) indicated that the model was responsive to morphological differences in different genotypes.

About one-third of total leaf area was fully developed at the time of panicle initiation. One to 3 lower leaves may also have senesced by that time. Following

panicle initiation, the remaining leaves expanded in succession. Simultaneously, the lower leaves continued to senesce. By soft dough stage 8 to 12 functional leaves were present, at hard dough stage, additional leaves were lost. By the time the grains attained physiological maturity, the remaining functional leaves turned yellowish brown or attained senescence (Arkin *et al.* 1976).

The leaf growth of a sorghum crop can be measured in terms of dry weight of leaves and leaf area of whole plant per unit ground area. As leaves intercept solar radiation, leaf area index (LAI) is used by crop physiologists for crop photosynthesis and growth analysis (Yoshida, 1972): $LAI = \frac{\text{Sum of leaf area of all leaves, cm}^2}{\text{ground area of field where the leaves have been collected, cm}^2}$.

In sorghum all the exposed green leaves are measured for LAI. This indicates the magnitude of leaf area relative to the ground. For example, if LAI=3, the crop has a leaf area thrice as large as the ground area. LAI greater than 1 is needed to cover the ground surface because all the leaves are brighter, flat and not in the same plane to cover the ground surface. LAI increases with the age of the crop and reaches its peak around flowering. After heading with the senescence of leaves, LAI declines.

Leaf area of the sorghum crop could be measured with the help of an automatic leaf area meter but the leaf area of an individual leaf could be measured in the following way (Ajmad, 1975):

$$\text{Leaf area (cm}^2\text{)} = \text{length (cm)} \times \text{breadth (cm)} \times 0.74.$$

The product of leaf length (L) and maximum width (W) is highly correlated with the actual area (A) of fully developed leaves. The formula $A = L \times W \times 0.75$ estimate the area of most individual leaves with reasonable accuracy but tends to overestimate the area of small leaves (Bueno and Atkins, 1981). Fourth leaf from the top shows good correlation with total leaves, but no single leaf accurately reflects the leaf area which is influenced by genetic and environmental factors (Bueno and Atkins, 1981).

A study on 4 sorghum genotypes during the rainy season of 1981 showed that there was a gradual increase in leaf area from 15-30 days after emergence, but a sharp rise from 30 - 45 days. From 45-60 days, leaf area showed slight decline later, followed by a sharp one due to senescence of leaves (unpublished, Fig. 4.23).

Water stress effects on leaf growth

Several reports show that water stress affects leaf growth considerably. Sivakumar *et al.* (1981) reported the LAI differences in sorghum in an alfisol and vertisol, and also under irrigated and nonirrigated conditions. Under irrigated conditions LAI increased up to 3.5 in vertisol, but reached nearer to 4.0 in alfisol under nonirrigated conditions. LAI did not show any difference in alfisol and vertisol. This shows that leaf area development is directly affected by water stress.

Slatyer (1973) stated that the growth of a plant organ depends on cell division followed by expansion and differentiation of individual cells. Uptake of water and nutrients, synthesis of structural materials and metabolites and transfer of substances between cells, are all related events. One of the most commonly observed effects of water deficits on plants is a reduction in growth with the effect being most pronounced in organs that are actively growing at the onset of water stress. Both cell division and cell expansion are known to be very sensitive to water

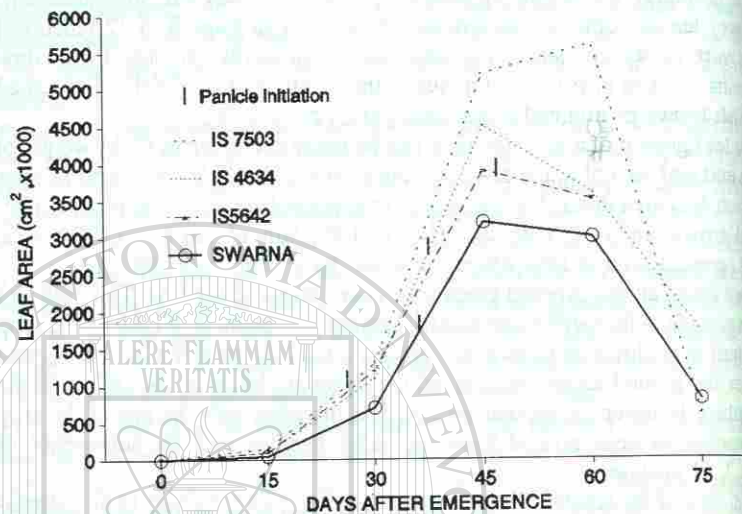


Figure 4.23 Development of leaf area in leaves of glossy and nonglossy lines of sorghum (unpublished).

deficits as measured by a decrease in plant cell number and their size (Boyer, 1968, 1970; Acevedo *et al.*, 1971; Clough and Milthorpe, 1975). Hsiao (1975) suggested that the rate of cell division may decrease as a result of decreased cell expansion. With regard to plant adaptation to limited water supply, the turgor pressure acts as the physical force for cell enlargement. The driving force for cell stretching and yielding of the cell wall is the turgor pressure (Lockhart, 1965). Therefore, to maintain a steady growth rate, the rate of water uptake must be equal to the rate of cell wall formation. Before either of these events can take place, turgor pressure should drop inside the cell. If there are no volume changes, this drop in turgor must be brought by a decrease of stress in the cell wall which is a phenomenon of stress relaxation (Yamamoto *et al.*, 1974). Stress relaxation seems to be the primary event in cell enlargement, while uptake of water and cell extension occurs only afterwards. If the threshold turgor is relatively high, a small drop in turgor may reduce the rate of cell enlargement. For cell elongation to be irreversible, synthesis and deposition of new cell wall material must occur. In addition, the initial growth of the cell wall appears to be under metabolic and hormonal control (Yamamoto *et al.*, 1974; Green and Cummins, 1974). Subcellular changes that occurred in sorghum leaves during increasing water stress and subsequent rewatering are described by Giles *et al.* (1976). Stomata closed, abscisic acid levels were elevated as well as the amount of starch in the bundle sheath. Chloroplasts were reduced by decrease in water potential. Swelling of the outer chloroplast membrane and reorganization of the tonoplast to form small vesicles from the large central vacuole occurred under decreasing water potential. On rewatering, large amounts of starch reappeared.

Effect of water stress on leaf extension

Leaf extension patterns for grain sorghum were studied by Johnson (1967), who reported that LER of irrigated plants was low during night, reached mid-point around 8:00 to 9:00 am and attained its maximum between noon and 16:00 hours. The temperature varied between 15 to 18°C at night and 30 to 35°C at midday. Leaf extension is reduced little by water stress (ICRISAT, 1982; Seetharama *et al.*, 1980, 1982). Sánchez-Díaz *et al.* (1971, 1973) showed that there was no difference in leaf elongation between sorghum and corn under severe moisture stress.

Diurnal evaluation of leaf water potential (Ψ) of sorghum was studied in detail by Elias (1976) and was found to be related to changes in incoming solar radiation. With surface and an increase in energy flux, the rate of transpiration also increased and leaf water potential started to decrease. The incoming energy flux was highest around midday when transpiration was maximum and leaf water potential minimum; late in the afternoon, as the solar radiation decreased, Ψ increased. Elias (1976) showed that contrary to normal finding, the rate of leaf elongation under field condition was high when Ψ was low and *vice versa*. He found that the growth rate in sorghum was low at sunrise, increased between noon and 14:00, and decreased as the night approached. Turgor pressure (ΨP) decreased early in the morning but later increased, reaching its maximum midafternoon. This was the reason why rates of leaf extension at midday were extremely high. Elias (1976) interpreted that the osmotic adjustment played an important role through turgor in the high growth rates was observed. Other authors (e.g., Boyer, 1968) also reported that ΨP does not necessarily decrease with decreasing Ψ . Elias clearly demonstrated that the pattern of leaf extension is determined by the interaction of temperature and water status. When day temperatures were high, leaf elongation rate was reduced by a decrease in ΨP . The ΨP values measured from noon to 14:00 were usually high, and so were the rates of leaf elongation during these hours. Subsequently, he found that ΨP correlated well with leaf elongation rate under controlled conditions. Elias found the relationship between ΨP and LER to be positive. He found that high LER were associated with high ΨP and low LER correlated well with low value of ΨP . Elias (1976) also showed that within a sorghum crop canopy, the amount of transpiration declined from the top of the canopy to the ground, because of light interception by leaves. Hence, one would expect the upper leaves to transpire more actively and to have lower Ψ than the lower leaves. Leaf Ψ decreased with height up to the flag leaf during morning hours; in the afternoon, the flag leaf showed higher values than the leaf immediately below it. The causes for improvement in water status of the flag leaf in the afternoon were apparently related to stomatal operation. In most cases, the decrease in Ψ in different leaves was directly related to solar radiation. Fully exposed leaves had lower Ψ than those in the shade. It was indicated that leaf Ψ decreased due to osmoregulation, a drought avoidance mechanism resulting in the formation of more osmotically active cellular solutes (Stout *et al.*, 1978). Greater leaf senescence of nonirrigated crop is another drought avoidance mechanism to reduce transpiration requirements (Stout and Simpson, 1978).

Water stress extended the period of leaf and stem growth and inflorescence development, and led to decreased vegetative and reproductive growth in sorghum (Stout *et al.*, 1978).

The difference in stomatal conductance in sorghum under water stress was due to differences in osmoregulation rather than leaf tissue elasticity. A conceptual model of osmotic adjustment to a crop with increasing water deficit was developed (Wright, 1981).

CULM

The vegetative shoot apex consists of a single tunica and a massive corpus (Lee, 1974). The ultrastructure of the tunica and corpus and the young stem are different from the outer corpus with respect to the morphology of the plastids and development of vacuoles. Plastids in the tunica and outer corpus are small and the thylakoids are poorly developed. Protein and starch granules are usually accumulated inside the leucoplast in the inner corpus and underlying stem region. Starch granules are deposited in the stroma, while the proteinaceous granules are bound by membranes inside the plastid. The thylakoids of the plastid tend to aggregate together in the inner corpus and the young stem region. Endoplasmic reticulum plays an important role in the formation of vacuoles. Development of vacuoles take place by dilation of the cisternae of endoplasmic reticulum. Large vacuoles, presence of ergastic substance in the plastids, differentiation of plastids into leucoplasts are considered as important morphological expressions of cell differentiation. Tunica and corpus region are regarded as promeristem (Lee, 1974). Therefore, the stem apex consists of a superficial primordium forming the apical dome which is enclosed by ensheathing leaf primordia and developing leaves. Leaves are derived as lateral primordia from the base of the apical meristem.

The culm or stem is made up of a series of alternating nodes and internodes encircled by leaf sheaths. The stem is slender to stout with length varying from 0.5 to 5.00 cm, is broader at the base and narrower at the upper end. The node is enveloped by the leaf sheath and appears as a ring at the base of the leaf sheath. A bud is present at each node, except at the flag leaf and sprouts from alternate sides of the stem. Sometimes these buds may develop into axillary tillers. Basal tillers are formed at the first node (House, 1980).

Stem anatomy

Stem anatomy in sorghum is typical to that of grasses. In a transverse section the epidermis consists of cubical to boat-shaped epidermal cells with a thickened outer wall. The ground tissue consists of thin-walled parenchyma. The vascular bundles are joint collaterally and scattered in the ground tissue. Just below the epidermis, there is a continuous layer of sclerenchyma. The number of cell layers in the sclerenchyma band and thickness of cell wall show variation in different genotypes. In some genotypes, the hypodermal bands of sclerenchyma are connected to the sclerenchyma bundle sheath of the subtending vascular bundle. There are alternate bands of large and small vascular bundles below the hypo-

dermal sclerenchyma band. The vascular bundles towards the center are larger in size. Mechanical tissues in the outer vascular bundles are extensive, particularly in the peripheral region. The genotypes show much variation in internal structure which includes intensity of mechanical tissues, intensity and size of vascular bundles, etc. (Figs. 4.20-4.21). The various types of vascular bundles were described in detail by Patel *et al.* (1981) in sorghum (*Sorghum vulgare*). Mesocotyl shows a cylindrical vascular tissue with 4 to 6 collateral, endarch vascular strands and presence of large metaxylem vessels between the 2 adjacent collateral bundles.

Three layers of vascular bundles are recognized in the internode at the periphery to the central part. The outermost layer comprises a variety of bundles, the central layer of middle-sized, elongated fibrovascular strands and the innermost layer of small bundles.

In the stem, different types of vascular bundles are noticed: 1- large bundle ensheathed by sclerenchymatous mass on lateral and xylary polar ends and a voluminous phloic cap of sclerenchyma just beneath the epidermal layer, 2- similar to the first but without epidermal sclerenchyma sheath, 3- comparatively small with smaller xylary fibrous strands and the phloic cap equal in volume to that of the xylary sclerenchyma strand, and 4- smallest vascular bundles intermingles between the above 3 types with absence of phloic elements.

Nodal vasculature is most complex. Some bundles in the node lack sclerenchyma sheath. The structure of the inflorescence internode is different. The most striking feature is the absence of the subepidermal masses of very large fibrous strands, and shape and size of vascular bundles differ in internodal vascular

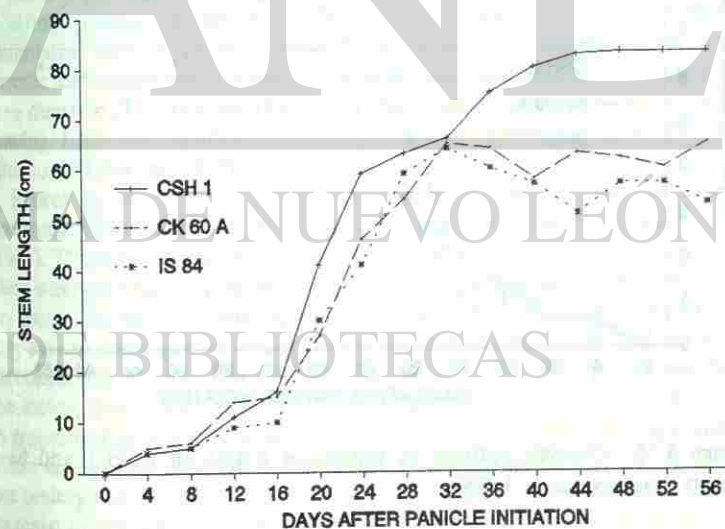


Figure 4.24 Stem elongation of CSH-1, and Indian hybrid, and its parents at different stages (rainy season, 1975).

bundle. Plants resistant to lodging had generally larger vascular bundles than lodging-susceptible types. The former were also more resistant to senescence of all tissues after freezing. This is associated with the number of total nonstructural carbohydrate in the resistant types. The lodging-resistant lines, which are generally perennial in nature than the susceptible types, showed higher dry matter values than the later at all growth stages. There was an association between lodging susceptibility and higher potassium and stalk protein (Esechie, 1975). Attempts could be made to correlate the intensity of mechanical tissue in the stem with lodging resistance.

Stem elongation

Elongation of the stem internodes begins shortly after panicle initiation and increases rapidly, starting with the short basal internodes, followed by the longer internodes and finally the peduncle. This produces the common sigmoid pattern of stem elongation with the rate of elongation at its peak at the flag leaf stage. There may be further increase in stem length following flowering in some cultivars due to continued elongation of terminal internode - the peduncle (Maiti, 1977; Figs. 4.24-4.25). As both leaves and stem contribute to the production of dry matter, the partitioning of dry matter in different plant parts will be discussed next.

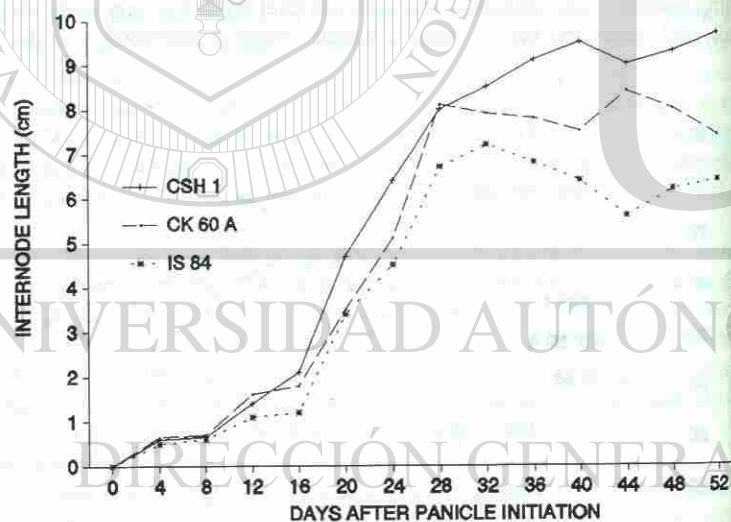


Figure 4.25 Growth pattern of internode length in CSH-1 and its parents (rainy season, 1975).

DRY MATTER DISTRIBUTION IN DIFFERENT PLANT ORGANS

Sorghum grain that shows a C4 dicarboxylic acid pathway of photosynthesis, which is believed to be an adaptation for efficient carbon fixation in environments where water limits growth. Arkin *et al.* (1976) formulated a dynamic growth model for sorghum. They concluded that at panicle initiation, all the remaining leaf primordia are laid and stem elongation takes place along with the extension and expansion of new leaves. This leads to a quick increase in leaf and stem dry weight.

The maximum dry weight of leaves was reached at the time of half bloom (stage 6) and of the culm between growth stages 6 and 7 (soft dough) or at full bloom. At the time of maximum culm weight, the plant had accumulated one half of its dry weight which then decreased until the grain was at hard dough-stage 6. After that, a gradual increase in culm weight occurred. Of the total dry matter, leaves contribute 20%, culms 20% and heads and grain 60% (Reeves, 1971, cited by Vanderlip *et al.*, 1973).

Studies on growth and nutrient accumulation in grain sorghum by Jacques *et al.* (1975) indicate that nutrient concentration (Zn, Cu, Fe, Mn) in blade, sheath, culm and head tissues generally decreased until maximum dry weight was reached, and then stabilized or decreased only slightly and gradually as grain developed. Whole plant nutrient concentrations decreased through most of plant growth (Jacques *et al.*, 1975).

Growth parameters throughout development for a range of sorghum hybrids in various planting regimes have been studied by Bueno and Atkins (1982). Net assimilation rate (NAR) was less affected by hybrid or sowing regime, average specific leaf weight was affected by plant density. Leaf area index (LAI) and leaf area duration (LAD) were affected by plant density and hybrid more than row spacing. LAD was significantly longer in the taller hybrid of a near isogenic line (Bueno and Atkins, 1982).

Flowering, development of grain, changes in moisture content and dry matter accumulation in the grain at different developing stages was investigated by Chang (1981). There was a rise in grain dry weight up to 40 days after pollination, and there was corresponding decrease in percent moisture (Chang, 1981). At anthesis, dry matter in the stem reached its zenith, after which it remained stable. There may also be some gain or loss in dry weight of stem (Maiti, 1977) if the need for carbohydrates is either less or greater than that available from photosynthesis in the leaves. Under such conditions, the stem serves as a store for carbohydrates in grainfilling or as a repository to store excess carbohydrates during grainfilling. There is relatively little dry matter distribution to the panicle as the panicle does not undergo rapid growth until the end of this period. During GS-3, the major increase of dry matter in the plant was in the panicle. About 50 % dry matter accumulated in the head, 25 % in the stem, and about 10 % in the leaf at the final stage. Dry weight of the stressed plants was about 75 % that of unstressed plant at maturity (Arkin *et al.*, 1976). Partitioning of dry matter to different plant parts

and its proportion varied in different genotypes (Maiti, 1986; Fig. 4.26). Carbohydrate content in sorghum culm changes with age of the crop. Total structural carbohydrate content showed increase the prebooting stage to anthesis (40%) in sorghum cultivar, with much increase in successive fractions. Diurnal variations reaching maximum at late afternoon, were most apparent at the prebooting stage. Glucose content in the upper culm declined, and sucrose increased at anthesis (McBee and Miller, 1982). Sorghum genotypes show variation in biochemical components (carbohydrate, wax, chlorophyll and HCN) at different growth stages (García-Mendoza, 1986).

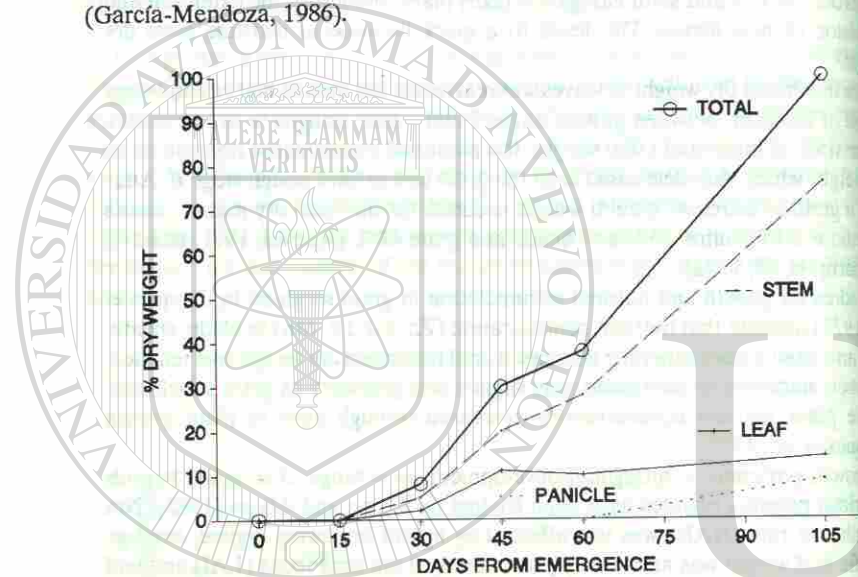


Figure 4.26 Partitioning of dry matter in different plant parts in IS-4634 during a rainy season.

COMPARATIVE LOOK ON STEM AND HEAD GROWTH IN DIFFERENT SEASONS

Maiti (1977) observed that the stems of all cultivars continue to increase weight after ceasing to gain height, attaining the maximum weight before the grain growth rate is reached. In post-rainy season, maximum stem weights were reached in 28 to 36 days after panicle initiation, but in late post-rainy season the period extended from 44 to 52 days. Comparative growth studies of head and stem in 3 seasons, rainy, post-rainy, and late post-rainy showed that dry matter production in stem and panicle was much lower in the post-rainy season than in the rainy season. A further decrease was registered in the late post-rainy season. Cultivar

22E was the only one that needed to draw translocates substantially on sources of assimilates to support grain growth which was most rapid in this cultivar. In rainy and post-rainy seasons, stem dry weight tended to be lower at anthesis; the loss was more after anthesis, but there was a sharp rise in panicle dry weight. This might indicate the mobilization of stem reserve to the developing grain in the head, as observed in the case of wheat (Rawson and Evans (1971) and Austin *et al.* (1977) and in barley (Gallagher *et al.* 1975). In late post-rainy season, there was considerable increase in stem dry weight and a negligible increase in panicle dry weight, indicating less translocation of assimilates. The favourable climatic condition prevailing in post-January caused considerable decrease in stem dry weight and negligible mobilization of stem reserves. As sink size and number were limited in late post-rainy season, the lesser demand in the panicles led to the intensification of photosynthesis in the stem. During post-rainy and rainy seasons, the sink size was high. This demanded more translocates and favoured mobilization of stem reserve to the sink (Maiti, 1986).

A comparative study on anatomy, morphology and growth characteristics of sorghum genotypes showed that the genotypes showed variation in morpho-anatomical characters in different growth stages, e.g. stomatal and epidermal cell frequency and correlations among these (Villanueva *et al.*, 1988).

GENERAL COMMENTS

From this comparative study of leaf and stem growth in sorghum we can deduce that the growth of these 2 plant parts - as in any other cereal - involves several dynamic growth processes. The initiation and early development of leaves of any taxon raise important and complex questions concerning the regulation of development processes in plants. It is difficult to interpret the developmental processes of leaf which leads us to some pertinent questions raised by Steeves and Sussex (1972):

1. Why does the peripheral region of the shoot give rise to outgrowth?
2. What mechanism regulates the placement of the outgrowth in the meristem?
3. What influences the outgrowth in such a way to cause them to be leaves?
4. What is the nature of the response to these influences that result in leaf development?

Several theories have been postulated to seek answers to these questions. However, the formation of leaf primordia is a major activity of the shoot lateral meristem. The change in growth pattern of a particular group of cells results in the formation of a distinctive organ - the leaf. The leaf has a definite developmental destiny characterized by its bilateral symmetry and elaborate structural specialization.

Leaf extension and the growth of sorghum leaves takes place due to active cell division and expansion of the leaf meristem located at the base of the leaf sheath. The growth of the stem is dormant until the transformation of vegetative meristem to reproductive meristem and the formation of all the leaf primordia. The initiation of the panicle meristem accelerates the growth of the stem. At this point,

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 panicle 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 the 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 a 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 DEVELOPMENT AND PRODUCTIVITY

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

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

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

Developmental morphology of the sorghum kernel has been studied by different researchers (Sanders, 1955; Paulson, 1969; Freeman, 1970). Caryopsis development at different parts of the panicle in sorghum was also studied by Dickinson and Eastin (1976). Maturity differences among sorghum varieties were considered to be due to the differences in response to photoperiod and temperature (Miller *et al.*, 1968 a,b; Quinby, 1967). Pauli *et al.* (1964) reported that planting date had a great effect on bloom and length of grainfilling. Significant correlation was found to exist between the duration of GS₂ and yield in sorghum (Dalton, 1967). Emphasis has also been laid on the possibility of improving yield in sorghum by extending GS₂. The decline in GS₂ days was associated with increasing temperature (Eastin *et al.*, 1975).

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

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	GS ₃
Stage 9	Physiological maturity: black hila layer formed at the hilar region of the seed	80-95	"

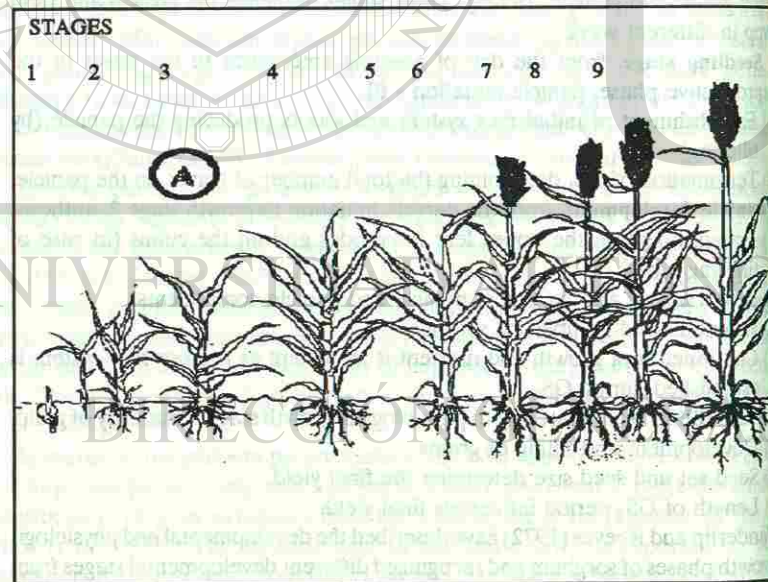


Figure 5.1 Sorghum development stages (Vanderlip & Reeves, 1972)

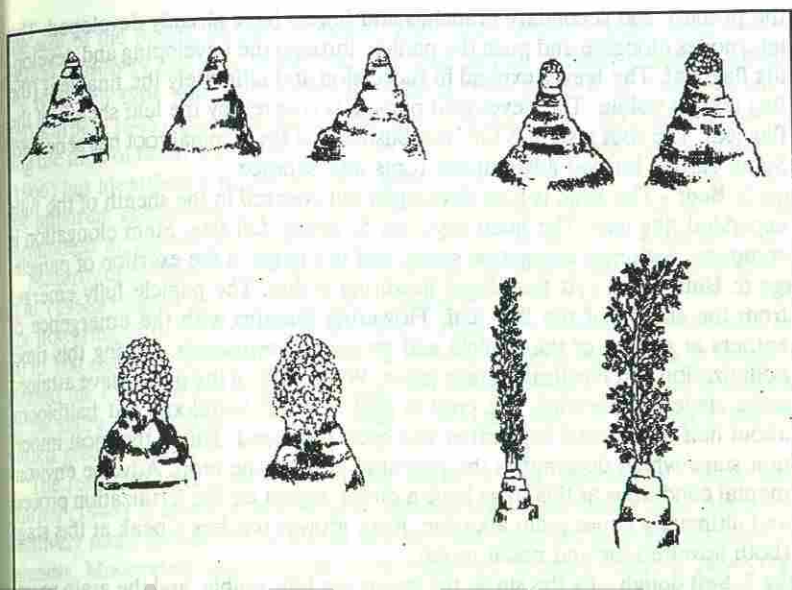


Figure 5.2 Sorghum panicle development stages (Vanderlip and Reeves, 1972).

- 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 well established 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. The internodes elongate and push the panicle through the enveloping and developing flag leaf. The leaves expand in succession and ultimately the final leaf (the flag leaf) is visible. The developed panicle is covered by the leaf sheath of the flag leaf. The root system is fully established and the seminal root has senesced. Some earlier formed adventitious roots also senesce.

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

Stage 6: Halfbloom - At this stage flowering is due. The panicle fully emerges from the sheath of the flag leaf. Flowering initiates with the emergence of anthers at the tip of the panicle and proceeds downwards. During this time pollination and fertilization take place. When 50% of the plants have attained some stage of flowering, the crop is said to be at halfbloom. At halfbloom about half of the total dry matter has been produced. This is the most important stage which determines the potential yield of the crop. Adverse environmental conditions at this stage have a direct impact on the fertilization process and ultimately cause grain abortion. Root growth reaches a peak at this stage (both adventitious and nodal roots).

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

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

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

Environmental factors influencing phenology

Sorghum is a short day, photoperiodically sensitive plant, but short day mutations in tropical sorghum in the southern parts of United States have led to development of relatively photoinensitive sorghum adapted to long day temperate environments (Eastin *et al.*, 1984). Eastin *et al.* (1984) have stated that floral induction in sorghum is caused by several factors, including genetics, photoperiod and temperature.

The understanding of the control of flowering and growth in sorghum is important, because it relates to grain yield in temperate climates (Quinby 1973, 1974). Since sorghum has a terminal inflorescence, the number of leaves initiated is controlled mainly by the time of floral induction (Sieglinger, 1936). This influences

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).

Stage	Rainy season (sown 18 Jun'77)				Postrainy season (sown 26 Oct'77)			
	Days	CSH-6 HU	Local Days	Local HU	Days	CSH-0 HU	Local Days	Local 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 sorghum (Seetharama, personal communication).

Growth stages	Factors that control it	Factors that determine yield
GS ₁		
0 Emergence	Soil temperature and moisture.	Growing plants, plantings/plant
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/plantings, seeds/panicle
GS ₂		
4 Flag leaf	Day length, air temperature, soil moisture.	
5 Boot	Same as (4)	Seed/panicle
6 Half bloom	Same as (4)	Seed size/weight
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 occurred. 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 reproductive

Table 5.4 Developmental sequence of panicle components (Lee *et al.* 1974) and developmental stages, GS₂ (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

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

Downes (1972) and Quinby *et al.* (1973) report genotypic variation in the time required to panicle initiation (PI). The development of the inflorescence is described by a number of researchers (Paulson, 1969; Doggett, 1970; Goldsworthy and Taylor, 1970; Downes, 1972; Lee *et al.*, 1974; Maiti, 1977). Floral initiation and developmental phases are largely controlled by photoperiod and temperature (Caddel and Weibel, 1971; Downes, 1972; Evans, 1960; Leng, 1951; Ross, 1959; Quinby *et al.*, 1973). PI takes about 30 to 40 days after emergence, but may vary from 19 to 70 days (House, 1980) and 33 to 45 days (Eastin, personal communication).

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

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

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

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 sporogenous 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 an 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 dissolves, 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

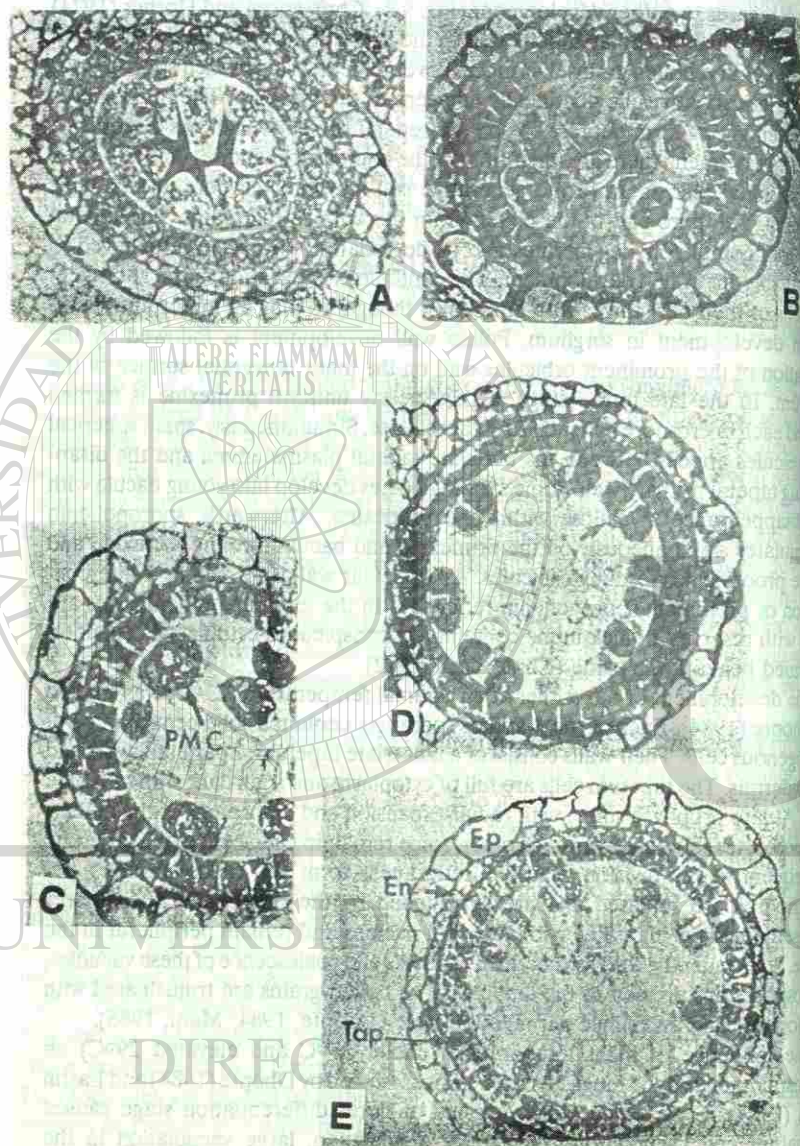
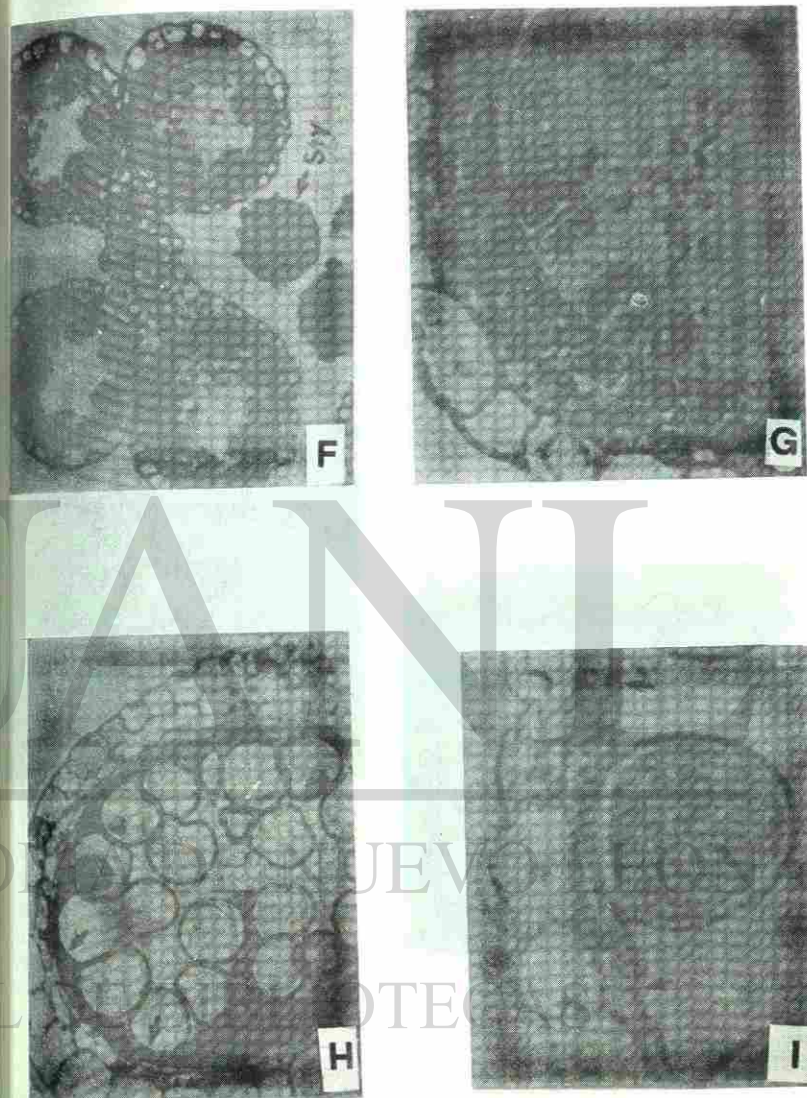


Figure 5.3 Transverse section through anthers, showing: A) A microsporangium, its central cell surrounded by the tapetum, two parietal layers and the epidermis. 470x. B) Dough stage of the sporangium with the destitution of the callus; each sporangium cell has its external surface in contact with the tapetum. 372x. C) Callus (C) separating each of the pollen mother cells (PMC) in the center of the loculus during the meiotic prophase. 400x. D) Developing wall, perpendicular to the tapetum, with a predominant callus in the loculus



(arrow). 375x. E) Formation of the triad with 3 distinct wall layers: epidermis (Ep), endotegium (En) and tapetum (Tap); all cells maintain contact with the tapetum. 370x. F) Loculus (1) 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.

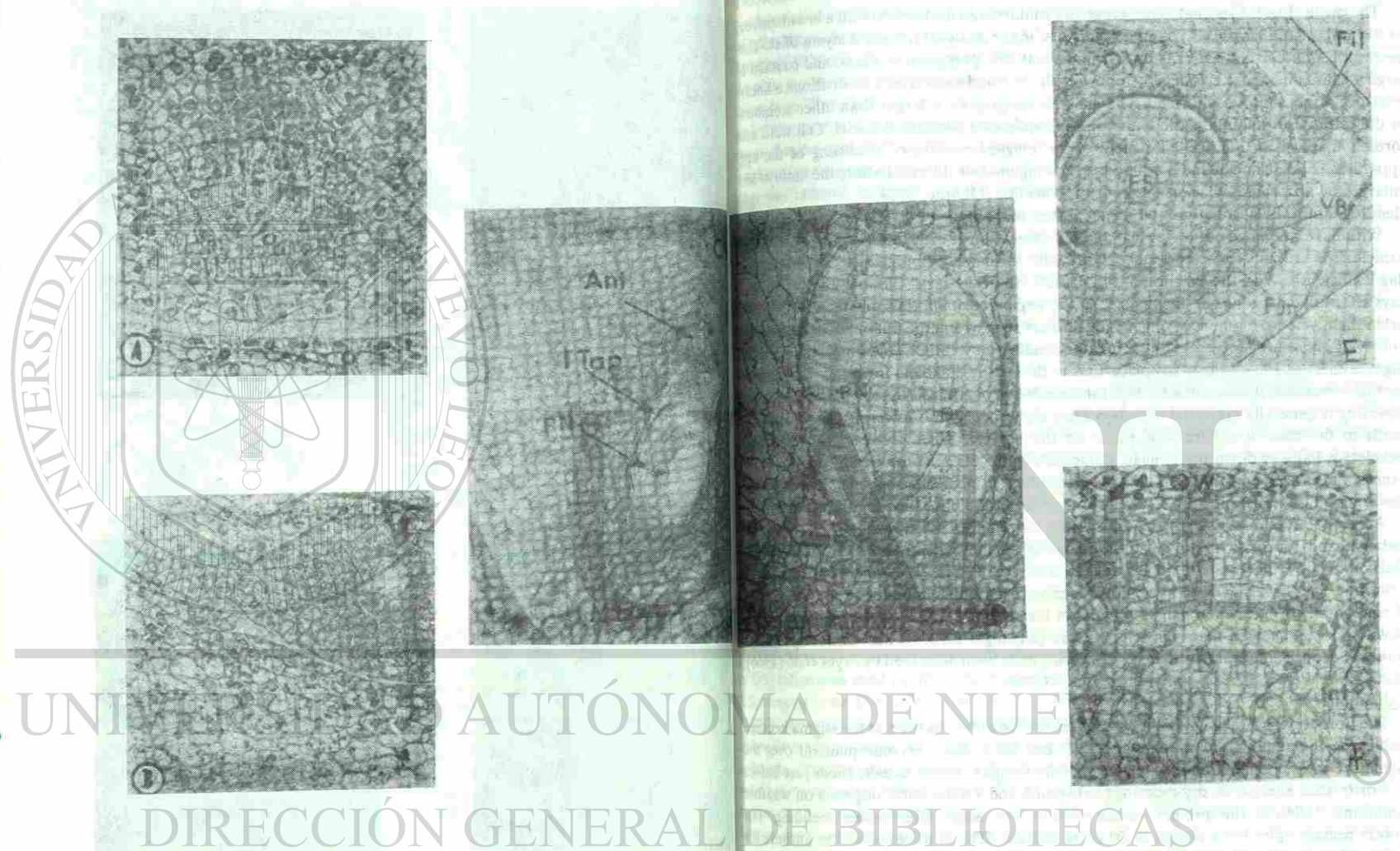


Figure 5.4 A) Functional megaspore (arrow) surrounded by degenerated ones. B) Functional megaspore during meiosis II (arrow) inside the embryonic sac. 538x. C) Complete embryonic sac with 8 nuclei, 3 antipodes (Ant) at the end of the chalaza (Cha) and 1 polar nucleus (PN) at the center; observe the development of the integument of the tapetum (T) surrounding the embryonic sac and the end of the micropilus (ME). 3311x. D) Egg cells (Eg) and the polar nucleus (PN) at the end of the micropilus. 398x.

E) Longitudinal section of the ovulus showing the ovary wall (OW) and the upper nuclear tissue (N) localized on top of the antipodes of the integuments (Int); observe the arrangement of the cells under normal conditions before fertilization. 323x. F) Transverse section of the ovary showing the embryonic 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 callus plugs in the pollen tubes and callose depositions in the pollen grains are associated with high temperature.

The ovule (Fig. 5.4) is anatropous, erect and solitary, and is attached with a broad stalk to the wall of the carpel. It has 2 integuments, inner and outer, each 2 layers thick. The megaspore mother cell arises from a hypodermal cell, polygonal in shape and contains a large nucleus and dense cytoplasm. Following the first and second meiotic divisions, a linear tetrad of 4 megaspores is formed. The chalazal megaspore is larger than other members of the tetrad. Subsequently, the embryo sac (functional) contains 8 nuclei. Cell walls are formed to form an eight-celled structure, the megagametophyte, consisting of the egg apparatus, 2 polar nuclei and 3 antipodals. During nuclear differentiation, the embryo sac 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, the panicle grows rapidly to the boot stage. Gradually, the panicle emerges after separating the flag leaf sheath. With the exertion of full panicle, anthesis starts. Flowers begin to open 4 days after full emergence of the panicle. At the beginning of anthesis, the tip of lemma and palea slightly open, filaments elongate and anthers start to emerge out of lemma and palea. Following the emergence of anthers, and depending on weather conditions, the feathery stigmas emerge. Flowering takes place first in the sessile spikelets from top to bottom of the inflorescence. It takes about 6 days for completion of anthesis in the panicle. Maximum flowering is generally noticed 3 or 4 days after anthesis begins. Flowering proceeds downwards to the base in a horizontal plane on the panicle. When flowering of the sessile spikelets is halfway down the panicle, pedicellate spikelets start to open at the top of the panicle and proceed downwards. The flowering phase of pedicellate spikelets overtakes the flowering phase of sessile spikelets before they reach the base of the inflorescence.

Anthesis (blooming) takes place during the morning hours. It normally starts around midnight and proceeds up to 10 a.m. depending on the cultivar, location and weather. Maximum flowering is observed between 6 a.m. and 8 a.m. Wet and cool days delay flowering. The flowering date for a cultivar is recorded as the number of days from the date of emergence to date when half the plants in the field are in half bloom (House, 1980). Downes (1972) showed that high temperature (day/night 32/28°C and 35/28°C) induces floret abortion. Temperature effects on flowering have been described by Fryer *et al.* (1980), 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 becomes visible, the filaments of the anthers elongate, and the anthers become pendant over the stigmas. It takes about 10 minutes for the spikelet to open. Pollen usually sheds just before or shortly after sunrise on dry mornings between 6 and 7 a.m., but it depends on weather conditions. Pollen in the anthers remain alive several hours after pollen shedding. The flowers remain open for a period of 30 to 90 minutes. The dehiscence of the anthers and pollen diffusion takes place through the apical pore.

Pollination takes place with the shedding of pollen grains on the stigma. Pollination starts first at the tip of the head and then progresses downwards, thus reaching the base usually 4 to 7 days later (Eastin *et al.*, 1973). A juice that the stigma secretes sticks the pollen grains falling on it. Pollen grains start to germinate on the stigma immediately after it is shed and remains receptive for a period of nearly 10 days. Sorghum is a self-pollinating plant and natural cross-pollination varies from 0.6 to 6% depending on the cultivar, but is usually about 6%. Pollination for crossing purposes should start soon after normal pollen shedding is over 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 GS₂ and GS₃, seed number and final grain yield in sorghum. As seed number is set during GS₂, 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 GS₂ and GS₃ (Eastin *et al.*, 1975). They showed that the duration of GS₂ was reduced 9% by higher night temperature, and increasing day temperature from 29 to 34°C reduced GS₂ by an average of 17%. The beginning 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 shown 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 GS₃ day was reduced in direct proportion to seed number reductions. Thus, the duration of GS₃ influences seed number and yield. Eastin (unpublished) recorded in 20 US hybrids GS₃ 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

(CSHI, 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 and 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 (Miller and Atkins, 1979). Greatest heterosis for embryo weight was manifested by the mediumheterosis hybrid. This may indicate that factors in addition to embryo size *per se* are involved in the expression of heterosis (Miller and Atkins, 1979).

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

Panicle growth:

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

Development of panicle components:

About 4 days after panicle initiation (PI), primary branch primordia were observed at the tip of the panicle in GS₁. This was followed by a continued formation of primary and secondary branch primordia and new spikelet primordia. These again differentiated to give rise to the development of floral parts. Successive spikelets started growing at progressive

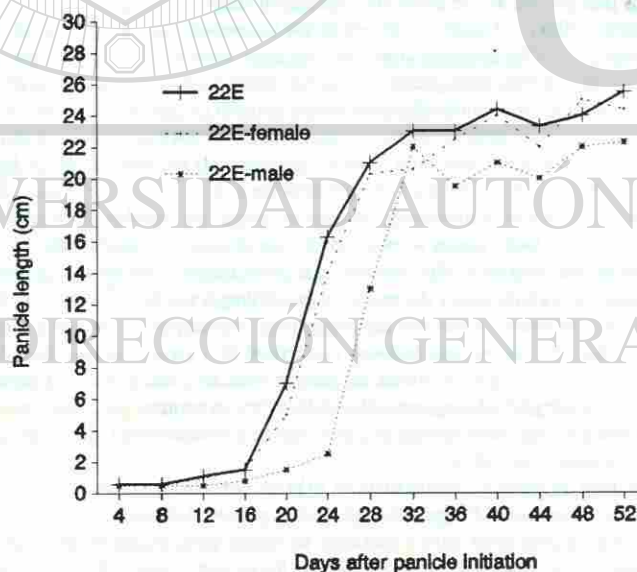


Figure 5.5 Growth pattern of panicle length (cm) in hybrid 22E and its parents in the rainy growing season 1975 (Maiti, 1977).

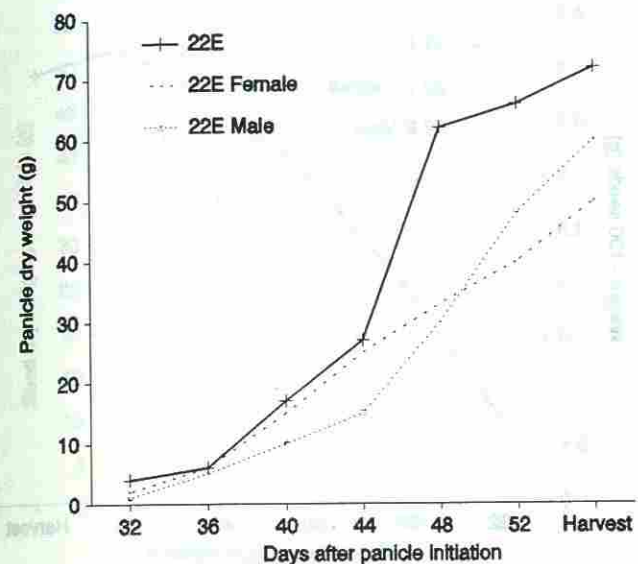


Figure 5.6 Pattern of dry weight increase of panicles (g) in hybrid 22E and its parents in the rainy growing season 1975 (Maiti, 1977).

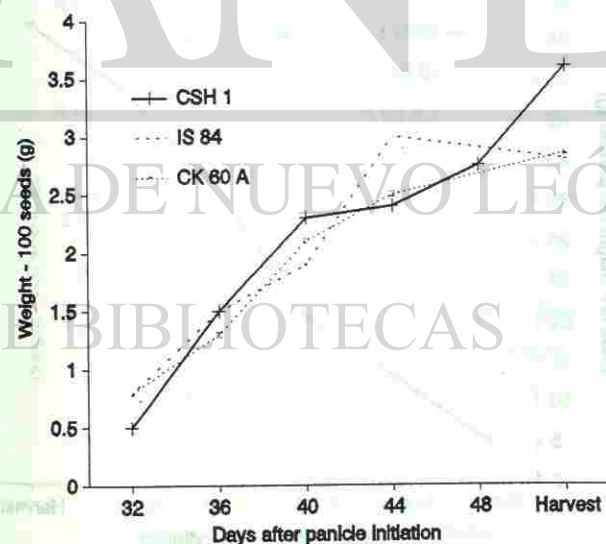


Figure 5.7 Pattern of grain dry weight change (g) in hybrid CSH1 and its parents in the rainy growing season 1975 (Maiti, 1977).

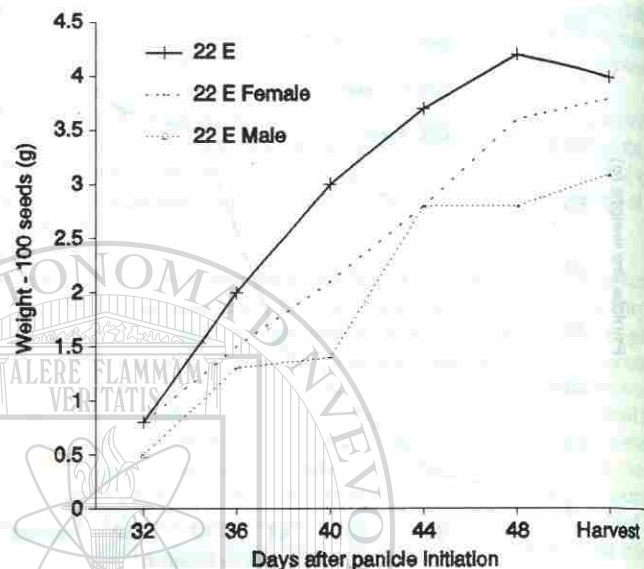


Figure 5.8 Pattern of grain dry weight change (g) in hybrid 22E and its parents in rainy growing season 1975 (Maiti, 1977).

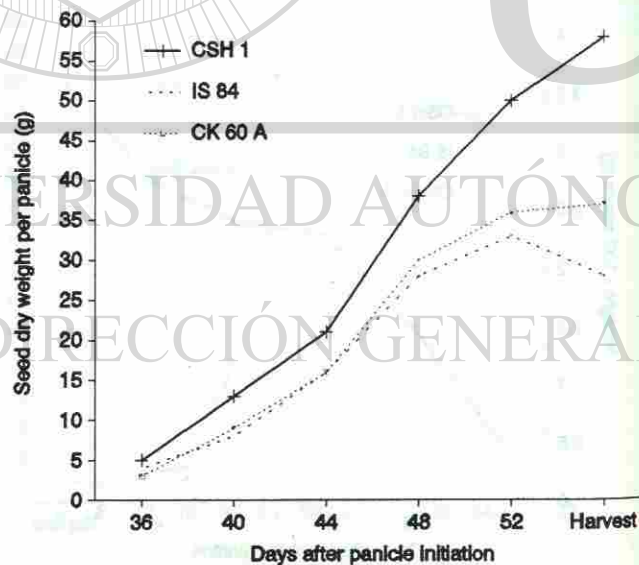


Figure 5.9 Dry weight accumulation of grain per panicle (g) in hybrid CSH1 and its parents (rainy growing season 1975; Maiti, 1977).

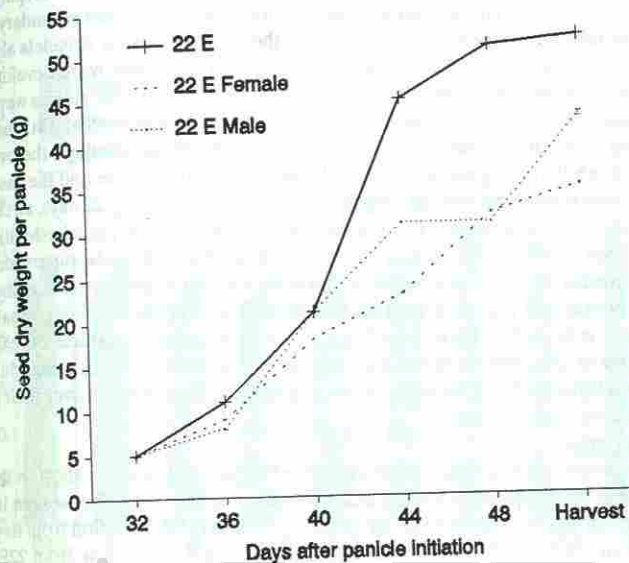


Figure 5.10 Dry weight accumulation of grain per panicle (g) in hybrid 22E and its parents (rainy growing season 1975; Maiti, 1977).

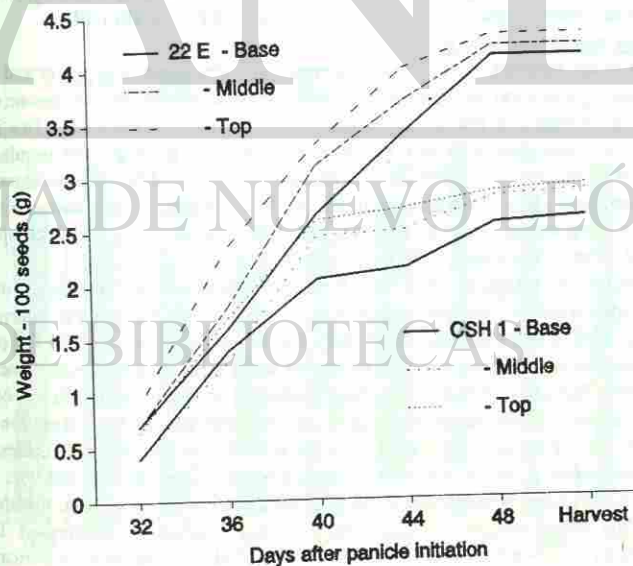


Figure 5.11 Pattern of grain dry weight change (g) at the base, middle and tip of the panicle in the rainy growing season 1975 (Maiti, 1977).

slower rates in about 8 days after PI, secondary branch primordia started developing on the primary branch at the tip. The sequence of development of primary and secondary branch primordia gradually progressed downwards. Thus, the development of spikelets also took place in basipetal order. By about 12 days, glumes, lemma and palea were developed at the tip, these were less developed at the middle of the panicle. At the base, only glumes were to be developing. After about 16 days, all the floral parts, except anthers and stigmas, were fully developed at the tip but less developed at the middle. Within 20 days, the ovary was fully developed, while the stigmas just started developing. At the middle and the base of the panicle, only anthers were developing; stigmas had not yet initiated. By 22 days, all the floral parts were fully developed at the tip, middle and the base of the panicle. Maiti (1977) reported that the development of panicle components in the hybrids superceded their parents. The hybrids and their parents have therefore shown distinct patterns in the length of vegetative period and rate of primordia differentiation. The high yielding capability of the hybrids was reflected in their superiority at an early stage of panicle development. Similar studies in other hybrids may validate this conclusion. Rao and Venkateswarlu (1976) and Gibson and Schertz (1977) have also shown the superiority of hybrids over their parents in terms of panicle development.

Seasonal difference:

The development time of different phenological stages of panicle is short in the rainy season, longer in early post-rainy season and still longer in late post-rainy season in the case of Hybrid 22E, which was very early maturing, showing considerable deviation from its parents in all the seasons. The developmental timetables of CSH1 did not deviate from 22E during the rainy season, but 22E showed much deviation from CSH1 in late post-rainy season. However, development of hybrid 22E was early in all seasons when compared to CSH1 (Fig. 5.12-5.13). The hybrids showed considerable decline in growth components in late post-rainy season compared to that in the rainy season (in 1976, India). The dry weight of panicle of CSH1 and 22E showed steep rise from 36-48 days after panicle initiation beyond which there was no significant increase in growth in rainy season. In late post-rainy season, growth of the cultivars declined considerably but increased again 52 days after PI.

Development and maturity of grain:

The grain is the ripened ovary with attached glumes. During development and maturation, grains pass through several distinct phases. The process starts with the formation of waxy fluid in the grain which is gradually condensed to the milky white stage. This in turn is converted to soft, and finally to hard endosperm stage. The grain growth terminates with the formation of black layer at the hilar region. The initiation of black layer shows a circular brownish ring which gradually encircles the hilum and gradually converts it into a black layer. Phloem parenchyma are blocked with mucilage and pectic compounds at maturity and form a black layer (Quinby, 1972a).

The structure and ontogeny of the black layer has been studied by Giles *et al.* (1976). The early appearance of phenolic compounds in the cells of the phloem parenchyma, accompanied with the formation of the dark patch adjacent to the transfer cells, is mucilage, possibly arising from the breakdown of slime strands, represents slime plugs in the sieve tubes. The appearance of mucilage coincided with the formation of pectic compounds and callose indicate the senescence of the phloem tissue and the cessation of assimilate translocation. The xylem gets separated from the phloem just below the lodicules, and the phloem forms a band which continues into the pericarp on the abgerminal side. The cento-chalazal pad lying between the band of phloem parenchyma and the transfer cells is made up of thin walled isodiametric cells and is neither crushed or compressed. The black layer appears as a brown band of tissue near the basal abgerminal side of pericarp in the area of transfer cells.

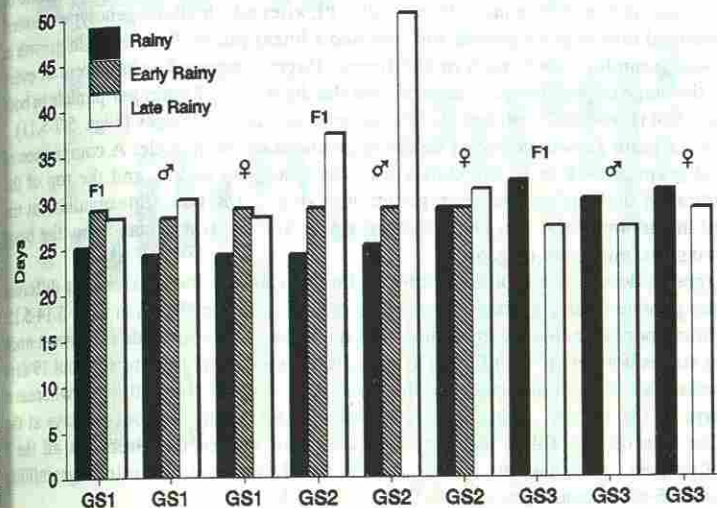


Figure 5.12 Growth stages of hybrid CSH1 and its parents in different growing seasons (Maiti, 1977).

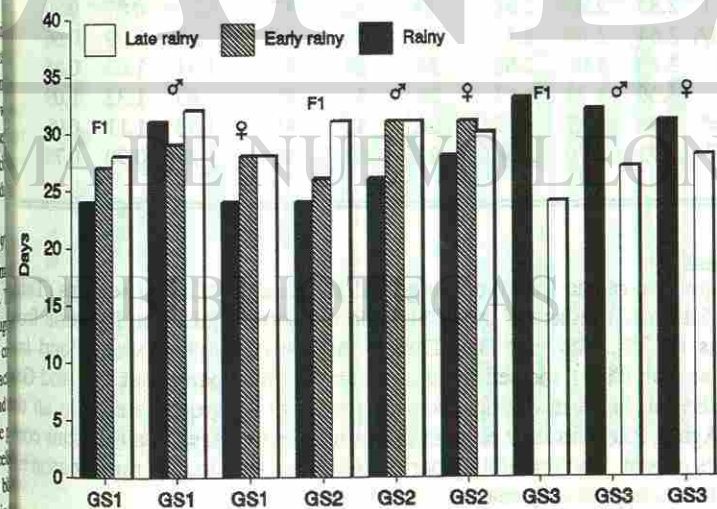


Figure 5.113 Growth stages of hybrid 22E and its parents in different growing seasons (Maiti, 1977).

A comparative study in rainy season on the grain dry matter (on the basis of 100 g weight) at different stages of both CSH1, 22E and their parents indicated that the rate of grain growth was slow at stages up to 36 days after PI, after which all the genotypes showed a more sustained rate of grain growth and assumed a linear phase. Rate of grain growth in CSH1 showed a similar growth pattern at different stages compared to its parent at the top stage up to the stage of physiological maturity, but the dry weight of grain per panicle in the hybrids (CSH1 and 22E) exceeded their parents at different stages (Figs. 5.7-5.11).

The rate of grain growth varied at different positions of the panicle. A comparison of the rates of grain growth in all the cultivars at the bases, the middle and the top of panicle indicated that the rate of grain growth was slow at the base, intermediate at middle and maximum at the top. Dry weight of grains at the top was maximum, the grain showing the minimum (Fig. 5.11).

The stages of development of grainfilling in the hybrids and their parents at different nodes of the panicle (starting from the top) also differed and are shown in Figs. 5.14-5.15. The grainfilling period increased gradually from the upper nodes towards the lowest nodes at different stages both in the hybrids and its parents. An individual grain took about 19 days for its transformation from the watery to the black layer stage at the first node, whereas it took 26 days at the bottom node. In 22E, it took 18 days at the top but 26 days at the bottom. The rate of grainfilling was higher in 22E than that of its parents at all the portions of panicle - the base, the middle and the top. In contrast, the rate of grainfilling was higher in IS-84, a land race, than in CSH1 (Table 5.5).

Table 5.5 Grain filling period and grain filling rate of CSH-1, 22E and their parents at different locations of panicle (top, middle, base) during rainy season 1975 (Maiti, 1977).

Genotype	100 seed weight(g)			Grain filling period (days)			Grain filling rate		
	Top	Middle	Base	Top	Middle	Base	Top	Middle	Base
CSH-1	2.83	2.80	2.61	24	32	37	1.17	0.87	0.70
CK60A	2.64	2.69	2.3	22	30	35	1.20	0.89	0.66
IS-84	3.40	3.01	2.82	24	29	33	1.41	1.03	0.85
22E	4.36	4.25	4.17	26	32	38	1.67	1.32	1.09
22E ♂	3.48	3.47	3.19	26	31	35	1.33	1.11	0.91
22E ♀	2.93	2.70	2.68	23	30	34	1.27	0.90	0.78

Growth stages:

A comparison of the length of the growth stages in 4 different seasons (Table 5.6; Figs. 5.12-5.13) indicated that CSH1 did not show significant deviation from its parents in GS₁, GS₂ and GS₃. During the early post-rainy season and the late post-rainy season CSH1 showed much deviation from its parents at GS₂ and GS₃ but 22E showed large deviations from its parent at all growth stages in all seasons. Again, 22E was very early in different growth stages in all seasons compared to its parent. The grainfilling period (GS₃) was very long in rainy season and very short in late post-rainy season.

Effect of weather on growth stage:

Table 5.7 shows the meteorological conditions under 3 stages for the 3

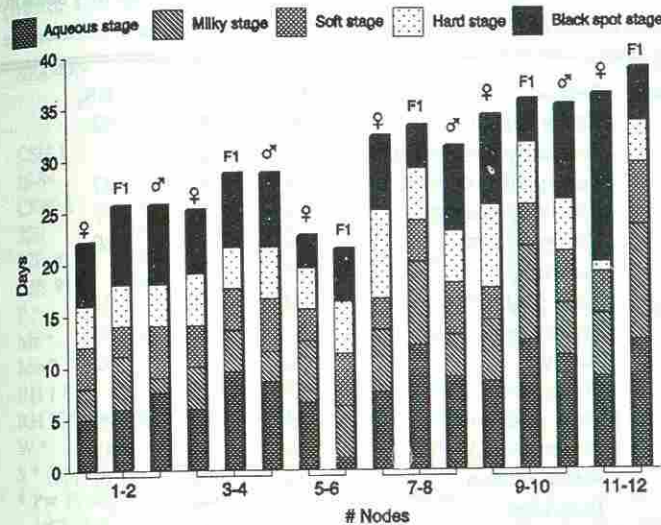


Figure 5.14 Grain filling stage of hybrid CSH1 and its parents in different nodes of the panicle during the rainy season 1975 (Maiti, 1977).

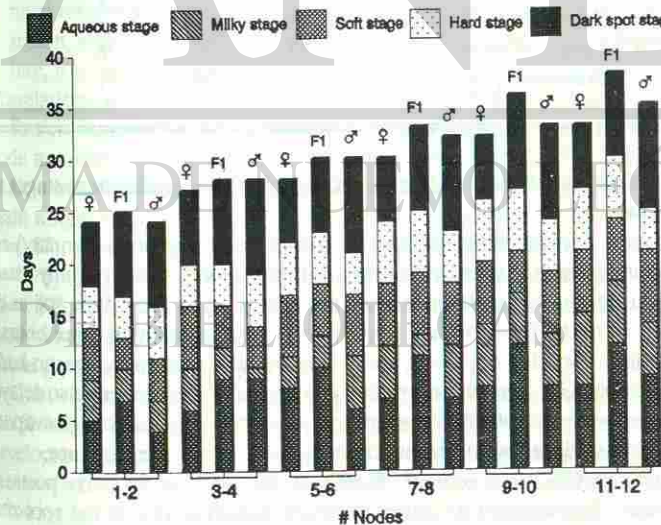


Figure 5.15 Grain filling stage of hybrid 22E and its parents in different nodes of the panicle during the rainy season 1975 (Maiti, 1977).

Table 5.6 Growth stages of CSH1, 22E and their parents in 4 seasons Patancheru, India (Maiti, 1977).

Genotype	Season	GS ₁	GS ₂	GS ₃
CSH1	Rainy season	25	24	32
	Postrainy season (early)	29	28	-
	Late postrainy season	28	37	27
IS84 ♂	Postrainy season (2)	28	41	31
	Rainy season	24	25	30
	Postrainy	28	29	-
	Late postrainy	30	50	27
CK60A ♀	Postrainy (2)	35	38	30
	Rainy	24	28	31
	Postrainy	29	28	-
	Late postrainy	28	31	29
22E	Postrainy (2)	26	42	31
	Rainy season	24	24	33
	Postrainy	27	26	-
	Late postrainy	28	31	-
22E ♂	Postrainy (2)	24	35	33
	Rainy season	31	26	32
	Postrainy	29	31	-
	Late postrainy	32	31	27
22 E ♀	Postrainy (2)	35	35	30
	Rainy	24	28	31
	Postrainy	28	31	-
	Late postrainy	33	30	28
	Postrainy (2)	26	39	31

The effect of meteorological parameters on growth rates at different stages discussed below:

GS₁: The delay in panicle initiation for the late postrainy seasons (January) and early postrainy season (September) trials compared with those of rainy season (June) might be due to insufficient moisture in the top layers of the soil as atmospheric demand (evaporation) was high in association with more hours of bright sunshine. Besides depleting soil moisture, the post rainy season had a delaying effect on GS₁. Development and expansion of leaves were also delayed though the crop was supplied with supplemental irrigation due to high evaporative demand associated with bright sunshine and higher temperature.

GS₂: Conditions in GS₂ were similar. However, in the case of early postrainy season's study (September) sufficient moisture was available in the root zone and this ensured that the growth rate was not affected.

GS₃: Fewer hours of bright sunshine and associated low day temperatures were the main causes for the delay in growth rate in the case of rainy season trials

Table 5.7 Weather and growth stages of sorghum in different seasons (Maiti, 1977).

SEASON	Summer 19.1.1976			Rainy 14.6.1975			Post rainy 11.9.1976	
	GS ₁	GS ₂	GS ₃	GS ₁	GS ₂	GS ₃	GS ₁	GS ₂
CSH-1	29	37	27	25	24	32	29	28
IS-84	31	50	27	24	26	29	28	26
CK60A	29	31	29	24	27	32	29	28
22E	29	31	24	24	24	34	27	26
22E ♂	33	32	29	31	26	32	26	31
22E ♀	29	30	26	24	28	32	28	31
P*	0	0.5	88	142	140	149	21	0.6
Mx*	26-30	>30	>35	>30	=30	25.3	>30	>30
Mn*	<15	<20	=20	>20	>20	>20	>20	16
RH I*	>80	>65	=50	>75	>85	>90	>80	>75
RH II*	20.4	<20	17	<55	>70	>70	>40	=20
W*	<10	<10	<10	>20	10.2	5.2	<10	<10
S* (approx.)	=9			=5			=8	

* P = Precipitation (mm); Mx = Maximum temp. (°C); Mn = Minimum temp. (°C); R.H. = Relative Humidity (I = morning, II = evening; %), W = Wind speed (Km/h), S = Sunshine (hr/day).

as the moisture was unlimited in this phase. The duration of the grainfilling period appeared to be lengthened by the prevailing lower minimum and maximum temperatures, low bright sunshine and low day temperature in the rainy season, while the reverse was the case during summer due to higher temperature, low relative humidity and bright sunshine.

Correlations among various traits related to panicle development:

Panicle length showed significant ($P < 0.05$) positive correlation with panicle node number ($r=0.95$), and primary branch length ($r=0.85$). Grain number per panicle was significantly related to the secondary branch number ($r=0.94$), and grain weight ($r=0.79$). Head weight was positively associated with grain number ($r=0.87$), grain weight ($r=0.99$), husk weight ($r=0.83$), and 100 seed weight ($r=0.78$). Days to anthesis showed negative association with primary branch length ($r=-0.87$). GS₃ days were found to show positive association with seed size (100 seed weight; $r=0.85$; Maiti, 1977).

Grain growth pattern (general)

Grain ripening is characterised by grain growth which is associated with increase in size and weight, change in grain color and leaf senescence. The process of grain development starts with the formation of watery fluid in the grain which is gradually converted to milky white, soft and finally hard endosperm stages. Initial growth following fertilization is free nuclear division in the endosperm. Following cell wall formation, the endosperm increases in size (unpublished; see Chapter 2 for details).

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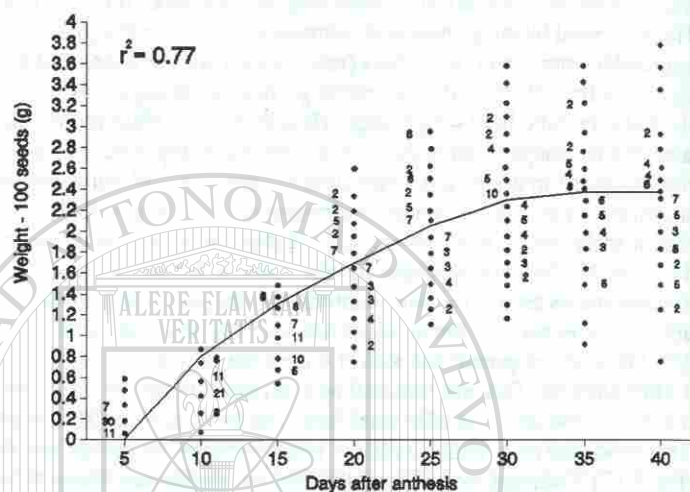


Figure 5.17 Accumulation of dry matter during the grain filling stage of (rainy season; Maiti *et al.*, 1979). (n = 50)

a set of 40 genotypes belonging to different taxonomic groups were chosen (Table 5.8). In order to study their behaviour in different seasons they were grown in early presummer (January) and postrainy season (September), 1976. The development of panicles from the date of initiation to physiological maturity was carefully observed, and the relationship between developmental stages and the yield components were also investigated. The mean number of days required for each developmental stage and yield components are given in Table 5.9.

Variability in developmental stages:

There was a wide range of variation in the vegetative and reproductive stages among various cultivars. For example, in the January experiment GS₁ ranged from 28 to 39 days, GS₂ from 24 to 64 days and GS₃ from 24 to 29 days. The number of leaves at panicle initiation ranged from 8 to 12, about 6-9 leaves were expanded at panicle initiation. Data on yield components also showed that the cultivars were widely variable. Panicle length ranged from 9.5 to 36.8 cm; node number from 12.5; number of primary branches from 95 to 71; number of secondary branches from 82 to 409; grains per panicle from 524 to 2307; grain weight per panicle 0.1 to 35 gm; and 100 seeds weight 0.55 to 4 gm. Out of 40 genotypes, only 20 flowered.

A close look at the developmental stages in both the seasons (Table 5.9) indicates that except for the three-leaf stage, all the developmental stages in the vegetative phase were delayed to a greater extent in the January planting than in the postrainy season crop. Stem elongation too was delayed in this season and

Table 5.8 Forty genotypes belonging to different taxonomic groups used in the development study.

Taxonomic group	IS	Origin	Taxonomic group	IS	Origin
Bicolor	714	USA	Durra-Feterita	7089	Equatorial
Bicolor-Kafir	658	USA	Durra-Feterita	7090	Equatorial
Caffrorum	183	USA	Durra-Kafir	3921	USA
Caffrorum-Roxburghii	2210	USA	Durra-Kaura	11025	Ethiopia
Caudatum	9743	Sudan	Durra-Roxburghii	4310	India
Caudatum-Kafir	127	USA	Grass-grains	1059	India
Caudatum-Kaura	7755	Nigeria	Guinese	3819	Africa
Caudatum-Durra	11574	Ethiopia	Margaritifera	8064	Japan
Caudatum-Guinese	3460	Sudan	Milo-Kaura	693	USA
Caudatum-Nigricans	8951	Kenya	Nervosum	11085	Ethiopia
Cernum	1054	India		11302	Ethiopia
Conspicuum	3818	Africa	Nervosum Broomcorn		113USA
Conspicuum	7999	Nigeria	Nervosum-Kaoliang	301	USA
Conspicuum	7630	Nigeria	Roxburghii	7276	Nigeria
Dochna-Collier	3648	USA		7818	Nigeria
Dochna-Amber	601	USA		6260	India
Dochna-Honey	633	USA	Roxburghii-Shallu	474	USA
Dochna-Leoti	640	USA	Subglabrescens	11150	Ethiopia
Dochna-Nigricans	2445	USA	Zera-Zera	3541	Sudan
Durra	4850	India			
<i>Shalense</i>		Bangkok/Tetraploid	Bangkok		

Table 5.9 Mean estimates of number of days for different developmental stages in 2 seasons (40 genotypes).

Stages	Postrainy season		Late postrainy season	
	Means	SD	Means	SD
1. 3-Leaf stage	4.65	0.48	4.22	1.25
2. 5-Leaf	18.86	1.72	14.41	1.39
3. Panicle initiation	30.68	9.76	30.70	2.56
4. Flag leaf	50.15	9.86	58.11	10.95
5. Boot stage	50.61	10.86	64.85	11.83
6. Half bloom	66.76	10.21	72.22	11.25
7. Soft dough	86.54	6.75	83.44	10.59
8. Hard dough	93.59	8.72	89.11	10.90
9. Physiolog.maturity	100.88	7.17	94.96	10.90
GS ₂	36.08	4.92	41.52	11.02
GS ₃	34.04	6.46	22.74	2.64

panicle initiation did not show any difference. Stem elongation took longer in January planting but the stages during grainfilling (GS₃, soft dough, hard dough and physiological maturity) were quite early. Seed size was reduced, which may lead to quick filling of the grain. Grainfilling also decreased to half during the postrainy season. The components of yield were lower in this season and affected panicle productivity (Table 5.10). This clearly reflected the effect of seasonal climate on crop phenology.

Table 5.10 Mean estimates of different yield components during the rainy season and the late postrainy season, 1976 (40 genotypes).

Component	Postrainy SEASON		Late postrainy	
	Means	SD	Means	SD
1. Plant height (cm)	174.88	6.89	-	-
2. Canopy height (cm)	134.26	53.83	-	-
3. Stem elongation (days)	26.93	4.63	34.15	11.44
4. Leaf number	-	-	15.85	2.51
5. Flag leaf area (cm ²)	95.04	7.59	-	-
6. Panicle length (cm)	24.59	13.46	29.41	32.23
7. Panicle dry wt. (g)	32.72	14.79	-	-
8. # secondary branches	-	-	256	85
9. Grain number/panicle	-	-	1100	476
10. Seed wt./panicle (g)	25	16.46	14.80	9.68
11. 100 seed weight (g)	2.67	1.17	1.96	0.79
12. Rate of grain filling per 100 seeds	0.22	1.27	0.09	0.04

The effect of weather on growth stages:

When comparing the differences in the GS₁, GS₂ and GS₃ periods in different taxonomic groups between postrainy and late postrainy seasons, the following conclusions can be drawn (Table 5.11): 1- on the basis of lifespan, the cultivars may be tentatively divided into 4 groups, A, B, C and D; 2- in all cases, GS₁ was longer in the late postrainy season; 3- in group C, GS₂ was longer during the late postrainy season; 4- in group D, GS₂ was longer during the postrainy season; 5- duration of GS₂ increased with high temperature and low relative humidity, bright sunshine hours and clear skies with dry air in the late postrainy season compared to postrainy season; 6- fifteen genotypes which did not flower in the postrainy season might be sensitive to high temperature and high atmospheric demands. These genotypes might be congenial only for the production of profuse vegetative growth rather than reproductive growth; 7- in all cases, GS₃ was shorter in the late postrainy. This might be due to prevailing high temperature, low relative humidity, longer day length, more hours of bright sunshine, clear skies and dry weather in the late postrainy season than in early postrainy season. All these unfavorable atmospheric conditions during late postrainy season might have led to reduction in grain size, quick grainfilling and low grain yield per panicle. Although the panicle

did not decrease in size, grain number and grain weight were much lower. This indicated that the unfavorable weather caused abortion of grains during the late postrainy season; 8- it may be assumed that high frequency irrigation was required in late postrainy season to cope with the high atmospheric demands prevailing in that season.

Table 5.11 Crop maturity of different sorghum genotypes in 2 seasons.

Days to maturity	Postrainy season	Late postrainy season
	IS No.	IS No.
80	633	8064
80-90	3951, 3460, 80644 7090, 3851, 3460, 301 9743, 1059, 13	310, 601, 3541, 127
90-100	Bangkok tetraploid, 2210, 183, 4310, 601, 3541, 127, 7090, 474, 301, 474, 9743, 13, 658, 11150, 2445, 3818, 1059, 640, 2210	Bangkok, 183
100-110	3921, 4850, 640, 658, 11150, 633, 4850, 2445	
110-120	3818	

Crop maturity:

The cultivars showed considerable variation for maturity periods within and between seasons. With a few exceptions, cultivars falling in group A, B and D matured much earlier in the rainy season than in the postrainy season. Cultivars showed shifts in their maturity status in the 2 seasons. A few cultivars (IS 474, IS 3460, IS 9743 and IS 4850) were fairly stable at the maturity stage in both seasons. During the postrainy season, many of the genotypes matured at 90-100 days, but a fairly large number did so between 80-90 days. Although many of the developmental stages were delayed in the late postrainy season, the maturity stage was reached early in many genotypes due to quick grainfilling. All the genotypes falling in group C (except IS 4850, IS 3921) were late in reaching physiological maturity. In other groups, with few exceptions, they matured earlier (Table 5.12).

Relationship among developmental stages (postrainy season 1976):

Some of the developmental stages showed significant correlations among themselves. Stem elongation phase was positively correlated with boot ($r=0.44$), half bloom ($r=0.43$) and soft dough ($r=0.46$). Flag leaf showed a significant negative relationship with panicle initiation ($r=-0.56$), flag leaf emergence ($r=-0.50$) and boot stage ($r=-0.46$). Days to anthesis showed high positive correla

tion with the total number of leaves ($r=0.86$) and stem elongation ($r=0.96$). *Re et al.* (1984) made a regression approach for prediction of sorghum phenology (GS_1 , GS_2 & GS_3).

Yield components:

A common method of examining the potential of sorghum grain yield is to measure the total dry weight and dry grain yield and then compute the harvest index (HI):

$$\text{Harvest index (HI)} = (\text{Dry grain yield}) / (\text{Total dry weight})$$

$$\text{Dry grain yield} = (\text{HI}) \times (\text{Total dry weight})$$

A HI of 0.5 or more is an indication of high yields. Of all the components, the number of grains per branch is the most important. Panicle size, number of primary and secondary branches, grain weight, grain number per panicle, number of heads per unit area could be considered the yield components of sorghum and understanding their interrelationship is a key to improvement of sorghum. The degree of relationship among the yield components would determine the importance of a particular component. Weather conditions, cultural management and nutrient supply greatly influence yield components. *Eastin et al.* (1984) stated that development limitations seems to be critical in grain production in terms of high temperature stress. Aspects of yield components are discussed by different authors (*Kambal and Webster, 1966; Stickler and Pauli, 1961; Blum, 1970a; Quinby, 1973; Beil and Atkins, 1967; Fischer and Wilson, 1975b*). Effects of temperature on yield components are well documented (*Tateno and Ojima, 1976; Chowdhury and Wardlaw, 1978*). Grain number per head was significantly altered by temperature over the range of temperature (day and night) from 21/16°C to 26/31°C and 30/25°C to 36/25°C; *Chowdhury and Wardlaw, 1978; Downes 1972*). Yields were markedly reduced at higher temperatures (30/25°C to 35/25°C) due to a reduction in grain weight (*Tateno and Ojima, 1976*). High temperatures during panicle development may reduce seed number per head and grain yield (*Heinrich, 1981; Ogunlella, 1979*).

Castleberry (1973) studied the effect of light energy available per plant on sorghum grain productivity by a series of thinnings. He observed that yield decreased until thinnings were done past floral differentiation (FD). Seed number per head increased sufficiently to maintain yield until FD, while the plant population was decreased by one-fourth (at about 2 weeks after PI). After this, population could not compensate in terms of seed number per unit of land area and an increase in seed size could not compensate seed number loss (*Eastin et al., 1984* but *Ogunlella (1979)* demonstrated that weekly exposure to elevated night temperatures in the field, 5°C above ambient starting from PI, have reduced yield and seed number per head. Therefore the week after floral differentiation is the most sensitive to elevated night temperature. *Dhopte (1984)* demonstrated the deleterious effect of elevated night temperature on microsporogenesis and megasporogenesis, resulting in poor seed set. *González-Hernández (1982)* showed that temperature and water stress interactions in sorghum.

Eastin et al. (1984) stated that sorghum is relatively insensitive to heat and water stress during the vegetative stage, but stress have variable effects during panicle development, the most sensitive period being about 3 to 6 days after anthesis during microsporogenesis. Stress at post anthesis at 7 to 9 days cause restriction

in seed size and seed number.

Relationship among different panicle components: The number of primary branches showed less positive correlation with panicle length ($r=0.46$). The number of secondary branches was positively associated with the number of primary branches ($r=0.59$). Grain weight per panicle was highly associated with the number of secondary branches ($r=0.49$) and the number of grains per panicle ($r=0.55$; unpublished).

Relationship between growth stages with panicle components: During the summer, the different panicle components like the number of grains per panicle ($r=0.51$), weight of grains per panicle ($r=0.50$), 100 seed weight ($r=0.51$) and number of primary branches ($r=0.53$) were significantly associated with GS_3 duration ($P<0.01$). Stem elongation was found to be significantly correlated to GS_2 duration ($r=0.98$). Days to maturity was found to be a function of leaf number, flag leaf, GS_2 and stem elongation ($r^2=0.97$). GS_3 duration was a function of number of secondary branches, number of grains per panicle and grain weight per panicle ($r^2=0.36$). Grain number was found to be linearly correlated with the number of secondary branches ($Y = 17+0.13X$, $r^2=0.51$). Grain number was found to be a function of secondary branches, primary branches, GS_3 and grain weight ($r^2=0.58$). Grain size (100 seed weight) was a function of the rate of grain filling ($Y = 0.28+19.1X$, $r^2=0.89$). Grain weight showed relationship to secondary branches, grain number per panicle, primary branches and GS_3 ($r^2=0.39$). It was again found to be correlated to duration of grainfilling ($r=0.50$). Therefore, the rate of grainfill and duration of effective grainfill were both correlated with panicle productivity. Grain number and effective grainfilling period were not correlated with days to anthesis, which suggests that these characteristics were independent of maturity. Days to maturity was found to be a function of flag leaf stage, leaf number, GS_2 and stem elongation ($r^2=0.93$; unpublished).

GENERAL COMMENTS

The transformation of the vegetative apex to the reproductive apex is the most important phenomenon in the life cycle of cereals. Temperature and photoperiod are the 2 important factors controlling this internal autonomous progression, when crops are grown under optimum soil moisture and nutrient conditions. This change in the formation of a completely dissimilar structure is a hormone controlled phenomenon and guided by photothermal interactions prevailing in the growing season of the crop. This phase represents the cessation by 1 group of genes and the initiation of activity by another (*Milthroe and Moorby, 1976*).

Most sorghum genotypes seem to be short day plants and on the basis of their response to day length, they can be grouped into photoperiod-insensitive, obligate photoperiod-sensitive, and facultative photoperiod-sensitive. Photothermal interactions play an important role in controlling flowering of these 3 groups. For this reason, temperate sorghum behave differently when grown under tropical environments. To break this tropical-temperate barrier, a suitable crossing program should be adopted in order to develop cultivars for broad adaptations.

This approach could give greater impetus to the sorghum crop improvement program. In the tropics, photosensitive sorghum grows very tall in the rainy season and often produces a large number of leaves and a few productive heads. To avoid this, photoinensitive sorghum are generally preferred.

As yield is the primary goal of the breeder, optimum growing conditions are essential for the expression of a crop's full genetic potential. Significant yield improvement has been achieved in different crops, but only under high input situations. In these favorable environments, the potential yield is determined during the early stage of inflorescence development and the panicle meristem is capable of producing the optimum number of florets to their full genetic potential. This is simultaneously substantiated by the optimum photosynthetic efficiency of a leaf attained during the vegetative stage. Nevertheless, it is very difficult to provide congenial growing conditions in most semiarid regions of the world. Often, crops are prevented from expressing their full genetic potential. The productivity of a panicle is drastically reduced due to several unfavorable environmental conditions like lack of water, low nutrients availability, salinity, high temperature, etc. Therefore, major research efforts need to be directed to screen genotypes which could express their optimal genetic potential under unfavorable field conditions.

In substantiation of this, under water stress situations, the growth and development of panicles is affected to an extent by the intensity of water stress at different stages of development. Under severe water stress when cell division is of paramount importance, spikelet differentiation tends to stop but under moderate stress situation, differentiation may be delayed not suspended. Under severe water stress failure of stem and internode elongation leads to poor or no exertion of the panicle. There could be a drastic reduction in floret number, thereby impairing the final productivity of the panicle and crop. Water stress affects the germination of pollen and growth of pollen tubes on stigmas. During grain development, water stress affects the sustained growth rate of grain. This ultimately leads to poor seed setting and filling of the grain and drastic reduction in seed size. It also has a direct effect on seedling establishment (Chapter-3). Therefore, drought avoidance trait with its capability to complete panicle development and anthesis within a short span of time is an adaptive mechanism. Lines could be selected from a group which express better panicle growth. These could be incorporated in a crop improvement program.

A full understanding of the reproductive apex and its interaction with environmental factors could provide some clues for the selection of cultivars and genetic improvement of the crop.

The maximum yield is determined by the potential of a crop variety and its adaptation to a particular environment. At present, breeders look for a dwarf plant with a compact panicle. However, in a tropical environment, compact panicle provides a favorable environment for the infestation and disease, like grain moths and earhead bugs. A lax panicle provides less opportunity for the development of the biotic stress. The focus of research should be to increase grain number per panicle and grain weight rather than evolving a dwarf plant prone to infestation. An ideotype in sorghum needs to be formulated for better adaptation in a particular environment.



ROOT DEVELOPMENT AND GROWTH

INTRODUCTION

Physiologists are more interested in the above ground portions of plants which play the central role during photosynthesis in plant metabolism. Very little attention is given to studies on the growth and function of root systems. This is partly due to the unavailability of an efficient technique for the extraction of roots from the field. Considerable variation in the expression of the size of roots occurs under different environmental conditions (Russell, 1977). Due to the difficulties involved, most research endeavors concerning root studies are conducted in greenhouses, growth chambers, rhizotrons and a few are based on observations in the field (Kaigama *et al.*, 1977). It is not possible to make a complete analysis of the growth and function of either roots or shoots unless the interrelationship between them and their behaviour in edaphic systems is taken into account (Russell, 1977).

Different techniques have been adopted to study root development in different crops. In sorghum, soil cores are taken from the field with the help of tubes to study depthwise distribution of roots and to correlate the relationship between root and the above-ground portion of the plant at different morphological development stages. Root morphogenesis and early growth have been done mostly in hydroponic culture (Blum *et al.*, 1977 a,b), sand culture (Nour and Weibel, 1978), and glass house pot culture (Hackett, 1973). Böhm (1977) described and compared different methods of root observation, both destructive and nondestructive in a natural environment in mini-rhizotrons. The use of clear tubes buried in the soil, or mini-rhizotron, has been described by different authors (Waddington, 1971; Böhm, 1977). Böhm (1977) stated that mini-rhizotrons required less time for data collections compared to other methods. Other methods have been adopted for the study of root system in different crops (Newmann, 1966; Marsh, 1971; Tennant, 1975; Voorhees, 1976; Sanders and Brown, 1978; Foale and Upchurch, 1982).

An endoscope introduced into a transparent tube and placed into the soil before sowing has been used for direct observation of root distribution and intensity of root colonization (Martens and Clauzel, 1982).

The root system of sorghum plants grown in soil measured at 9, 14 and 17 days from sowing indicate the low average diameter of the root number and the very high extension rate. Sorghum appeared to maintain a stable relationship between the overall number, length, surface area and volume of its root (Hackett, 1973). In sorghum, both under irrigated and non-irrigated conditions a rapid penetration

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of root was observed early in the growing season (Kaigama *et al.*, 1977). Traces of roots were observed at depths of 140 to 150 cm 6 weeks after emergence. A greater proportion of total root dry weight accumulated at deeper depths in non-irrigated than in the irrigated sorghum, but the rate of dry matter accumulation of both roots and tops was higher in the irrigated treatment. Response of sorghum plant rooting to irrigation timing showed that daily irrigation resulted in as rapid and as deep a root penetration as did less frequent irrigation (Merrill, 1976). In this study, root length and dry weight yield were 20 to 30% higher under daily irrigation. Merrill and Rawlins (1979) also reported that increases in root length and root dry matter were larger under irrigated rather than under non-irrigated conditions. A video recording system in mini-rhizotron has been developed by Upchurch and Ritchie (1983) for observations of root systems and densities at different depths, which gives good correlation with those determined by soil sampling.

Studies on root and shoot development by Heatherly (1975) in silt loam soil in Missouri indicate that root density in the 0-30 cm soil region reached maximum at 5 weeks after planting and then remained relatively constant until 2 weeks before maturity, declining rapidly afterwards. Below 30 cm the time of maximum root density occurred 2 to 4 weeks later. More than 80% of the root mass was located in the top 30 cm of soil. Depth-wise distribution of dry matter at maturity has been investigated by several researchers (Bloodworth *et al.*, 1960; Teare *et al.*, 1973). Sorghum root could reach a depth of 150 cm or more (Miller, 1960; Nakayama and van Bavel, 1963; Lavy and Eastin, 1969; Mayaki *et al.*, 1976; Kaigama *et al.*, 1977). Lateral extension of the root over 2 m from the crown was reported by Lavy and Eastin (1969). Different reports indicate that more than 80% of sorghum roots are concentrated within 30 cm below the surface (Bloodworth *et al.*, 1960; Nakayama and van Bavel, 1963; Stone *et al.*, 1973; Saint-Clair, 1977; Jordan *et al.*, 1979 a,b; Thomas *et al.*, 1979). Burch *et al.* (1978) reported that the early maturing variety (Ruse) of sorghum approached maturity, its root distribution decreased in soil layers below 10 cm depth whereas in other varieties (Bragg), which matured 2 weeks later, maintained a deep root system and continued to deplete water down to 120 cm. Deep penetration of some roots could be related to drought resistance and that drought resistance could be improved by selecting genotypes with deeper roots. The more drought resistant cultivars were stated to have heavier roots, greater root volume and higher root/shoot ratio than the drought susceptible lines (Nour and Weibel, 1978).

The seminal root arises with the emergence of the radicle through the coleoptile. The seminal root is mainly responsible for the establishment of seedlings. Crown roots develop from the basal stem nodes and provide anchorage to the plant by spreading laterally before growing downward. Blum *et al.* (1977) reported that the early maturing sorghum genotypes initiated the adventitious roots earlier than the later maturity genotype. This character may be useful as a selection criterion for improved crop establishment. Jordan *et al.* (1979 a,b) reported that the seminal root of sorghum seedlings growing under field conditions usually deteriorates as the crown root system become established. They reported that in field situations the appearance and rate of elongation of crown roots are influ-

enced by available soil water in the upper layer, usually limited under rainfed situations.

Studies on root systems of some Senegalese and American sorghum cultivars indicated that the former produced lower root weight than the American ones, and they showed better balance between root and shoot (Saint-Clair, 1977). This trend may be associated with adaptation to semiarid or dry environments. About 84% of the root weight were found to be located in the first 25 cm soil layer. Myers (1980) reported that the maximum root dry weight occurred at about the time of anthesis and argued that total root length and root mass were reliable criteria for root measurement. Genotypic differences in root development are desirable in sorghum (Blum *et al.*, 1977 a,b; Nour and Weibel, 1978; Jordan *et al.*, 1979 a,b; Jordan and Miller, 1980).

Root clipping has no significant effect on root growth and shoot growth. Compensatory growth within the existing root member was capable of maintaining root length and volume, but not root dry weight when crown roots were severely reduced (Jordan *et al.*, 1979 a,b). Under mulching systems root growth *viz.* root length, number of adventitious roots, volume of roots, dry weight of roots were found superior when compared to the control, both at flowering and harvest (Palanivel and Ramanathan, 1981).

Sorghum root growth is influenced by soil physical properties (Baligar and Nash, 1978). Germination and emergence of sorghum were delayed in finer aggregates. An increase in clay content reduced root growth, but an increase in aggregate size increased root elongation. Better root growth was observed in a sandy to sand-loam texture than clay to clay-loam texture (Baligar and Nash, 1978). Hewitt and Dexter (1979) concluded that smaller aggregates offer better nutrient availability per unit length of root. Deep ploughing before sowing increased root density and water use efficiency (Chopart and Nicou, 1976). Warsi and Wright (1973) reported that increasing nitrogen levels from 0 to 160 kg/ha increased root growth, specially during the early stages. Myers (1980) in a comprehensive review of the literature on root in grain sorghum states that most of the work has concentrated on mineral absorption using radioactive trace techniques (McClure and Harvey, 1962; Nakayama and van Bavel, 1963; Lavy and Eastin, 1969), and water use (Blum and Naveh, 1976). Hemsath and Muzurak (1974) studied the growth of seminal roots at an early seedling stage and found elongation positively correlated to the water potential of the soil which indicates the effect as that of soil resistance. The effects of partial and complete removal of the primary seminal root of sorghum during the first 6 days of growth after germination were investigated by Chotib *et al.* (1976) by growing seedlings in modified Hoagland's solution. No significant differences were found in various growth components between the untreated controls and plants with induced defective primary root systems. Damage occurring 1 or 2 days after primary root emergence is compensated by the rapid appearance and growth of adventitious roots due to the availability of seed reserves. A vigorous primary seminal root is not a requirement for normal growth of the hybrid sorghum.

A strong coordination between shoot and root characteristics has been reported in sorghum (Bhan *et al.*, 1973; Jordan *et al.*, 1979 a,b; Wright *et al.*, 1983). Mirhadi

et al. (1979) reported that there was some relationship between the growth of internodes and rooting behavior in sorghum plants: with the emergence of the 2 leaves on the plant, one of the lower internodes reaches its maximum length. At this time, root primordia began to elongate from the base of the internode. A similar phenomenon was observed in lower internodes of corn plants (Kobayashi and Mizutani, 1970).

The total number of primordia and elongated roots increased with high soil water content, but the increase was higher after a ten-day drought, once the 2nd leaf had emerged (Mirhadi and Kobayashi, 1979). There was no significant difference between control and wilting treatments at all growth stages for the number of roots. Teare *et al.* (1973) reported that water stress was apparently responsible for reduced activity of nitrate reductase, which eventually reduced the ratio of protein to amino acid.

González-Rodríguez (1989) established a model in a quantitative estimation of root growth in sorghum, both under irrigated and non-irrigated conditions. The number of first and second order roots could be predicted from the branching length of the seminal roots since constant rates were observed. Root dry weight and length were strongly associated with leaf area and shoot dry weight.

Many studies have dealt with the distribution pattern of roots in different soil profiles, but they have not taken into account the whole root system and its components, which is only possible in solution cultures, sand cultures or in microtome sections. Very few attempts have been made to study the whole root system of sorghum, pearl millet and other cereals in soils. The following account is based on the study (unpublished) by the author to investigate the development of the whole root system under different conditions. The results are discussed in the light of available literature.

DEVELOPMENT OF THE ROOT SYSTEM

After emergence, the radicle elongates to give rise to the seminal root. The mesocotyl elongates from the base of the radicle and the mesocotyl roots emerge from the coleoptile node (Fig. 6.1). Sorghum has a fibrous root system, and mesocotyl roots increase in magnitude when seeds are planted deep in the soil.

Two types of root are generally identified in sorghum: seminal roots which arise directly from or below the germinating seed, and the adventitious or mesocotyl roots that arise from the axis between the node of the coleoptile and the base of the radicle (Fig. 6.2a). At later stages, about 30 days after emergence, crown roots arise from stem above ground (Fig. 6.2b). However, from the standpoint of physiological function both types of roots function in a complementary manner (Williams, 1962). Injury to the seminal root can lead to enhanced activity of crown roots. The root system in sorghum is similar to that of other cereals. As growth advances, both adventitious and nodal roots develop branched secondary roots which in turn develop tertiary roots and so on. On the basis of the stage of development and their function, the root systems of sorghum could be distinguished into their constituent components. The following observations

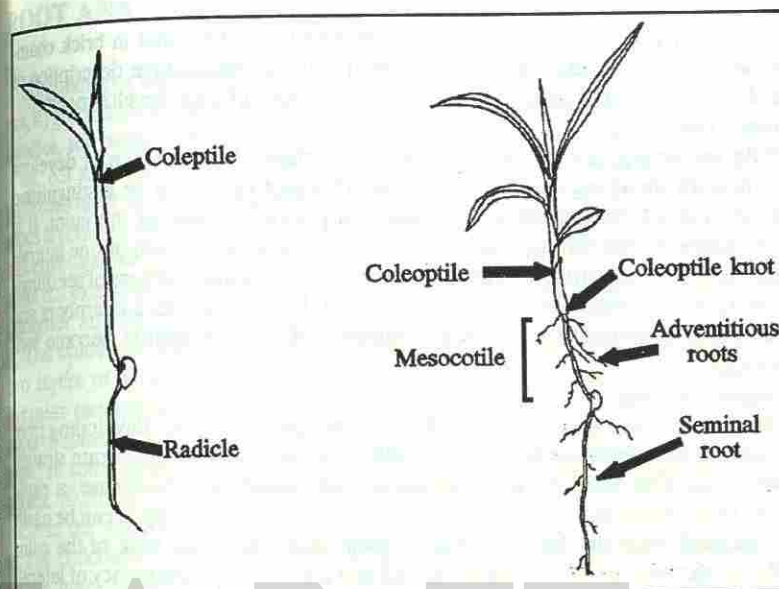


Fig. 6.1 Development of primary roots.

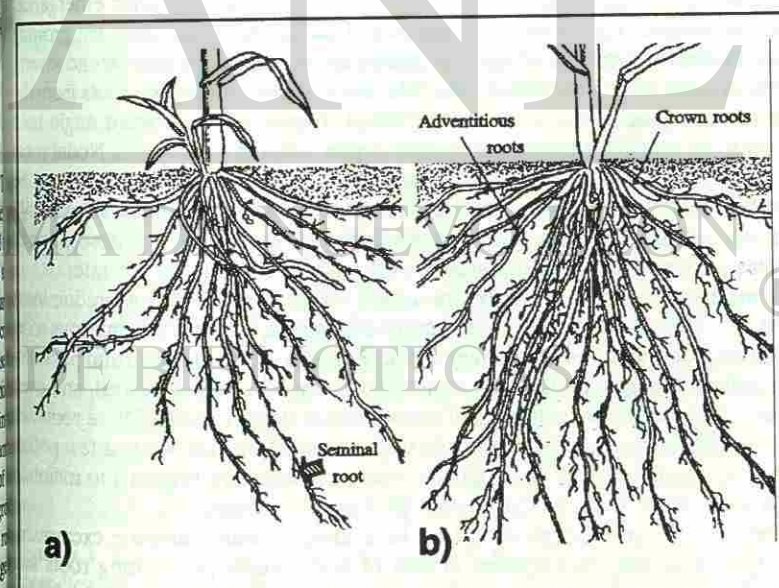


Fig. 6.2 Root system of sorghum in the field (a) at panicle initiation stage, (b) at boot stage.

by the author are based on his experiments both in the field and in brick chambers. Moreover, González-Rodríguez (1989) made a quantitative description of root development and established a statistical model of root development.

Seminal root

With the emergence of radicle through coleorhiza, the primary root develops directly from the elongation of the radicle. This root can easily be distinguished from the rest of the members by its continuity with the base of the culm. It is much narrower near the culm with scanty laterals and has a bunch of fine laterals at the distal end. This root is mainly responsible for the establishment of seedlings. The seminal root was found to survive up to 45 days both in brick chambers and in the field, by which time the other members of the root system become well developed.

Adventitious roots

Besides the main seminal root, a few adventitious roots start developing from the base of the coleoptile while the seminal roots develop at a faster rate straight down if not obstructed by any mechanical impedance, in which case, a rapid growth of adventitious roots would be stimulated. Adventitious roots can be easily distinguished from the seminal roots by their thickness at the base of the culm, gradually narrowing towards the distal end and the increased frequency of laterals from the base to the distal ends. About 30 days after emergence, the activity of growth of adventitious roots becomes predominant. The adventitious roots are found to be quite active up to anthesis and start senescing thereafter.

Nodal or crown roots

These initiate from the base of the stem about 30-40 days after emergence when the seminal root is fully developed and the adventitious roots are growing better. Depending on the cultivar, the crown root development may extend several nodes. In some cultivars (Indian local 'Maldandi' types), the crown roots from the third to fifth node above ground were found to grow at an inclined angle until reaching the ground, growing downwards to give support to the stem. Nodal roots are green above ground and send profuse laterals while in the soil; they can be identified from by their stout nature and the few laterals at the base. After 100 days, the crown roots send many laterals deep into the soil for the absorption of nutrient as is evident from the growth and meristem activity of the laterals.

From anthesis up to maturity, the crown roots seem to take a predominant support function. Towards the middle of the grainfilling period, very few adventitious roots are active, but major nodals are very active. Towards the hard dough and physiological maturity stages, all the adventitious roots have already senesced, and even the major nodals show symptoms of senescence at deeper levels. These roots are found to give support only towards the upper layer of the soil, while a few nodals may survive and continue to supply the minimum moisture required to maintain the growth of the plant at the physiological maturity stage.

The root system in sorghum cannot be studied without elaborate excavations. In a field situation, root systems consist of both deeply penetrating roots and shallower horizontally extending roots, depending on irrigated and rainfed cultivars. Under irrigated conditions, horizontally extending roots are profuse while in rainfed soils, roots penetrate deeper.

ROOT ANATOMY

Sorghum root anatomy is typical of monocots. It is composed of i) outer epidermis, ii) ground tissue below the epidermis, iii) endodermis surrounding the vascular bundles, iv) radial bundles with alternate xylem and phloem bands, and v) pith (Figs. 6.3 and 6.4). The root anatomy of *Sorghum bicolor* consists of an outer cortex, a sclerenchymatous layer surrounding a cortex which is composed of outer soil parenchymatous layers without air cavities and the innermost layer, the endodermis. Endodermis envelops the central stele. The anatomy of nodal roots is similar to seminal roots but extensive sclerenchyma regions develop in both the hypodermis and stele (Sangster and Parry, 1976a).

The epidermis consists of a single layer of cubical cells subtended by one or two layers of large oval hypodermal cells. The cortex is made up of oval to irregular parenchymatous cells with considerable inter-cellular spaces. In older roots of some genotypes, the cortical cells elongate to assume a plate-like appearance. In some genotypes, there is a single layer of thick-walled exodermis in the cortex. A single layer of cubical or brick-shaped cells of cortical parenchyma encircle the endodermis.

The endodermal cells are barrel-shaped and are thickened with suberin on the inner tangential wall. The endodermal thickening varies with genotype. Silica crystals are present in the endodermal cells; their shape and size vary with cultivar and with the age of root (Figs. 6.5-6.8). Silica crystals are absent in some genotypes. The pericycle below the endodermis is composed of one or more layers

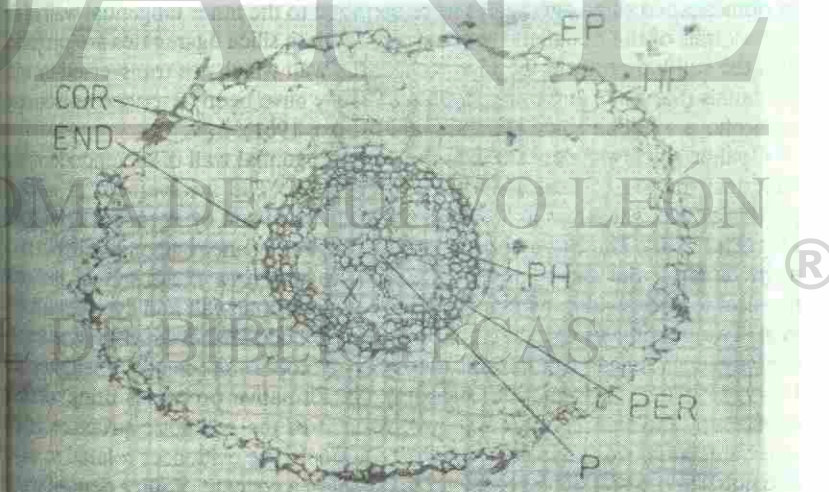


Figure 6.3 Transverse root section of a sorghum genotype showing the pattern of cortex cells and arrangement of vascular bundles. EP-epidermis, HP-hypodermis, COR-cortex, END-endodermis, PER-pericycle, X-xylem.

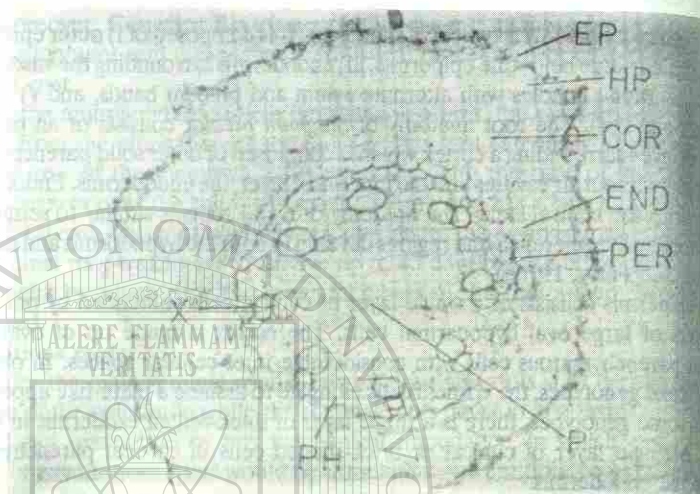


Figure 6.4 Transverse root section of another genotype showing the pattern of epidermal cell, cortical cell and vascular bundles. EP-epidermis, HP-hypodermis, COR-cortex, END-endodermis, PER-pericycle, X-xylem and PH-phloem.

of thickwalled sclerenchyma cells of which generally the outermost layer is highly lignified. Lignification varies in different genotypes. Solid silica deposits occur as domeshaped silica aggregates were confined to the inner tangential wall of the endodermis of the nodal and seminal roots. These silica aggregates are projected into the cell lumen from the inner tangential wall which are transversed by vascular pit canals (Sangster and Parry, 1976 a,b). They have been described as isotropic, amorphous, opaline silica (Lanning and Linko, 1961).

Opaline silica was deposited on the inner tangential wall of the endodermis as spherical masses of coalesced primary particles. The involvement of silica in particular drought stress in sorghum has been discussed by Ponnaiya (1960), Doggett (1970). The characteristic serial arrangement and regular spacing of silica aggregates on the inner tangential wall is regarded as the result of the physical forces developing over the entire endodermal wall and cytoplasmic face. Two hypothesis have been put forward for endodermal deposits, one involving physicochemical factors and the other protoplasmic control (Sangster and Parry, 1976 a,b). Information regarding the formative processes using electron microscopy indicate considerable involvement of the cellulose structure of the inner tangential wall (Sangster and Parry, 1976c). The evidences related to water and nutrient transfer across roots are in favour of a concept of silica deposit within the endodermis of sorghum by direct cytoplasmic involvement. Silicon is deposited on the inner tangential walls of the endodermis. In addition, discrete evenly distributed deposits varying in size partly fill the lumen of these layers. Some exhibit a number of smaller protrusions. These lumen deposits show protrusions

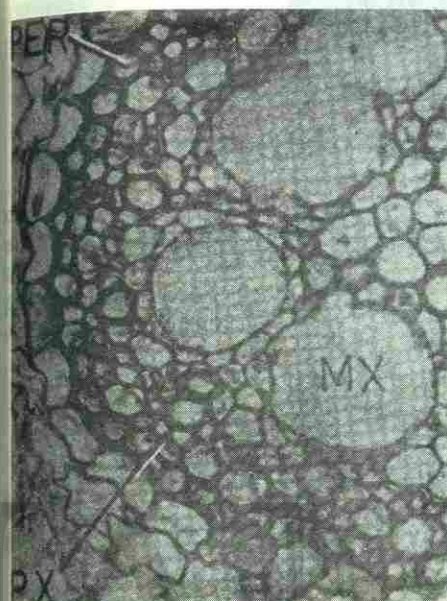


Figure 6.3 Transverse root section of CSH1 showing the thickening pattern of the walls of endodermal cells and pericycle. Endodermal silica crystals were not observed. PER-pericycle, PX-protoxylem, MX-metaxylem.

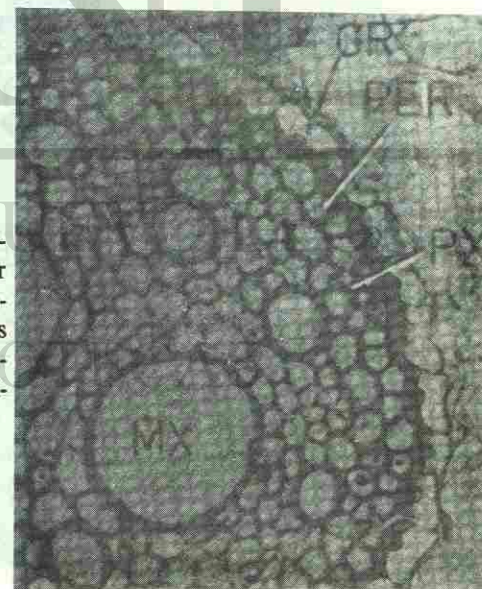


Figure 6.6 Transverse root section of IS-148, a sorghum cultivar showing highly thickened endodermal cell wall and silica crystals in the endodermal cell cavity. CR-silica crystal, PER-pericycle, MX-metaxylem.

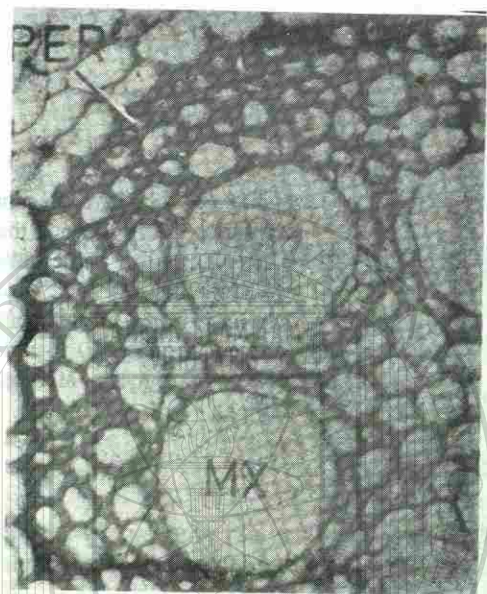


Figure 6.7 Transverse root section of *Dobbs*, a cultivar showing thickened endodermis, silica crystal and pericycle, thickened pericycle. PER pericycle, MX- metaxylem

Figure 6.8 Transverse root section of IS-301 showing highly thickened pericyclic cell and absence of silica crystals.

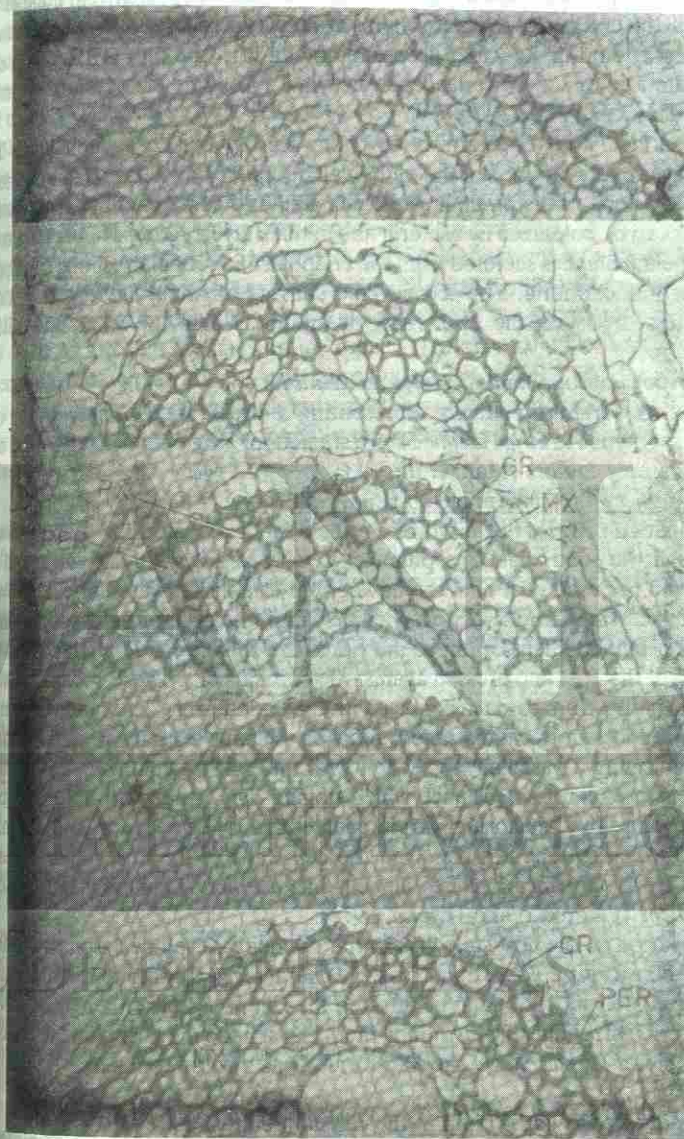


Figure 6.9 Transverse root sections of sorghum genotypes showing the pattern of cell wall thickening of the endodermis, pericycle and xylem vessels, and orientation and size of silica crystals.

and have a distinct granular structure in contrast to the very uniform pattern of the wall deposits (Parry and Kelso, 1975).

Xylem parenchyma surrounding the metaxylem may be thick- or thin-walled. The xylem and phloem show a typical radial arrangement, protoxylem bundles are present on the exterior of the metaxylem (exarch). The size, number and thickness of the metaxylem bundle varies according to cultivar. The pith is solid, with cells elongated compactly arranged parenchyma cells. The size of pith varies in different cultivars (Fig. 6.9).

Root surface and root hairs of sorghum secrete 2 types of mucilage. The fibrillar layer exists on parts of the outer wall of epidermal cells and on root hairs. It consists of long fibrils parallel to the cell wall and connected by anastomosing layers. This layer can be colonized by bacteria and in thick layers, groups of bacteria were found. The mucilage is secreted from the endoplasmic reticulum, Golgi apparatus, as well as mitochondria. The second type consists of small, heterogeneous and structureless drops on the distal part of the roots hairs (Werker and Kishor, 1978a,b).

Seedling root anatomy and *Striga* parasitization

Twenty-six sorghum cultivars representing a wide range of susceptible and resistant genotypes to *Striga asiatica* were studied for *Striga* parasitization and for root anatomy factors (Maiti *et al.*, 1984b).

Parasitisation on the susceptible sorghum root

Germination of *Striga* began with the radicle (or the haustorium) making its way out through the seed coat. The plumule grew very slowly at this stage and remained with the seed coat until the haustorium established vascular contact with the host root. The plumular axis was visible within the arch of the 2 cotyledonous leaves. The bulbous haustorium at the tip of the radicle made contact with the epidermis of the host and pressed against the cortical cells. These became disorganized and the haustorium came in contact with the endodermis. The outer tangential wall of the endodermis was disrupted, allowing the haustorium to penetrate into the stele, establishing a vascular connection with the host vascular bundle. In some cases, the presence of a substance which stained dark green with toluidine blue was noted when the haustorium was in contact with the endodermis. A chemical substance which softened or dissolved the cell walls of the host tissue was produced by the advancing haustorial cells in *S. asiatica* (Saunders, 1933) and *S. gesperoides* (Okonkwo and Nwoko, 1978).

The invasion of the host stele was by the tracheids developed from the xylem of the young haustorium. These tracheids were characterized by the spiral thickening (Rogers and Nelson, 1962) and penetrated the xylem vessels either by dissolving cell walls or by mechanically disrupting them. This made the host parasite connections complete. At this stage, the haustorium was almost double the size of the host stele.

Development of the haustorium in the resistant cultivars

In resistant cultivars, the attachment to the root and the penetration of the cortex by the haustorium were similar to the process in the susceptible cultivars. However, in the resistant cultivars most of the haustoria failed to penetrate the endodermis in contrast to the susceptible cultivars in which most haustoria were

successful in establishing vascular connections with the host root stele.

Many resistant cultivars were found to have thickening in the endodermal cell wall and the pericycle cells were also found to contain crystals. This can be observed in the resistant cultivar N13 (a local cultivar, Nandyal), in contrast to the susceptible CSH1 (an All India Coordinated Project hybrid). In another study, the course of development of thickenings was followed in these 2 cultivars in the absence of *Striga*. Cell wall thickenings in these 2 tissues as well as the presence of crystals was evident in N13 as early as 7 days after germination. In contrast, CSH1 had only negligible thickening in the endodermis and contained no crystals even 14 days after germination. By 28 days, there was only a small increase in thickening in the endodermis and pericycle of CSH1, whereas N13 accumulated considerable thickening materials, especially in the pericycle. In addition, several apparent responses to the invasion of the *Striga haustorium* were observed in certain cultivars. One of these appeared to be extra lignification in the pericycle cells at the point of contact of the haustorium with the endodermis in N13 and IS 4202. As a result, the haustorium appeared to become distorted and failed to penetrate the stele. In another resistant cultivar IS 8686 (SRN 4841), a few haustoria did penetrate the endodermis but on reaching the xylem, tyloses like occlusions from *Striga haustorium* were found in the xylem vessel.

Host root anatomy vs field resistance for *Striga*

Aspects of host root anatomy like thickness of the inner tangential wall of the endodermis, degree of lignification of the pericycle, and the frequency and size of crystals in the endodermal cells were studied in 26 selected cultivars. Generally, resistant cultivars showed a high degree of endodermal and pericyclic thickening and the presence of silica crystals, whereas susceptible ones showed less thickening and no crystals. Based on the overall score, all the cultivars in the resistant group had high or intermediate rating for all the 3 characteristics.

ESTABLISHMENT OF ROOT SYSTEM IN THE SOIL IN RELATION TO THEIR FUNCTIONS

Root system distribution in the soil is an indicator of the nutrient-uptake capability of a genotype. Sorghum roots are capable of penetrating the soil, 2 to 5 cm/day (Nakayama and van Bavel, 1963), reaching considerable depths quite early in the growing season. Kaigama *et al.* (1977) reported that sorghum roots of Pioneer 846 reached a maximum depth of 140 to 150 cm within 42 days after emergence. Myers (1980) found that the roots of both Pioneer 846 and RS 610 reached a depth of 135 cm by panicle initiation, 22 days after emergence. Both reports showed that a large part of the root mass was located within 15-20 cm of the soil surface.

Kaigama *et al.* (1977) showed that more than 90% of the total root weight was within 15 cm of the soil surface. Myers (1980) reported only 76-79% of the root mass in the 0-20 cm layer. It is practical, therefore, to restrict root sampling to the top 10-20 cm of the soil to get the real picture of root intensity of a genotype. Myers and Asher (1982) stated that sorghum roots remain active and capable of

nutrient absorption until very late in the growing season.

The plant root system plays an important role in determining the rate and amount of soil water available to the crop (Jordan and Sullivan, 1982). Blum (1974) stated that modification of the root system to extract greater quantities of soil water or to regulate the rate of depletion play an important role in drought avoidance mechanism. There is genetic variability for root characteristics in sorghum (Jordan *et al.*, 1979 a,b; Blum *et al.*, 1977 a,b; Wright *et al.*, 1983; No and Weibel (1978); Bhan *et al.*, (1973); Jordan and Monk (1980), therefore scope for selection for better root systems exists. The genetic variability is generally expressed in the distribution of growth (dry matter) between the shoot and root as well as behaviour of root axes and lateral branches. High root to shoot ratio in young plants is found to be correlated with superior drought resistance (No and Weibel, 1978; Bhan *et al.*, 1973). Research needs to be directed to study the value of specific root traits to drought resistance. Jordan and Sullivan (1982) state that a choice of the root 'ideotype' should be based on a thorough understanding of the seasonal pattern of water availability. Increased rooting depth tends to increase water availability (Jordan and Miller, 1980). Increased rooting density in the deeper layers of the soil surface allows greater absorption of water in the soil. Water in the soil is depleted more slowly when there is a serious water deficit. Deficits occur near anthesis, a sensitive growth phase, then deep rooting may contribute to yield maintenance, but a delay in water stress may avoid damage to the crop provided water is available to complete grain development. Deep rooting is considered to be an useful mechanism for crops grown on soils where deep profile recharge occurs during the off-season (Jordan and Miller, 1980). Passioura (1972) provided evidence that grain yield in wheat was highly correlated with water available at anthesis. Richards and Passioura (1981) showed genetic variability for xylem vessel diameter in wheat roots. Similar efforts need to be made in the case of sorghum (Jordan and Sullivan, 1982). Under drought conditions, soils in the shallow layers start drying from the surface, but the deep horizon of the soil may have sufficient soil moisture. Therefore, deep rootedness is a feature that facilitates drought resistance. High root-shoot ratio is also considered as an adaptation for drought resistance in rice (Yoshida, 1981; Jordan and Miller, 1982).

WATER AND NUTRIENT UPTAKE BY ROOT SYSTEM

The main function of the root system is to siphon water and nutrients from the soil for the growth of the plant. Solar radiation, temperature and humidity are important forces operating on the foliage and result in a constant demand for water by the plant. In order to maintain the normal vital activity of the plant, cells in the tissues should be turgid. Plants give out excess water through stomata by a process known as transpiration. The growth of plant depends on the efficiency of the root system of the plant to tap available water in the soil. Under drought conditions, when the shallow layers are depleted of water, the plant should have a deep root system to tap water from deeper layers of the soil. The rate of water absorption from a given soil volume should be proportional

to the effective total length or intensity of the root system. The high rate of water absorption leads to a more rapid decrease in soil water in the shallow layers; more water is available to the roots deeper in the soil. Details of the water uptake process is explained in Chapter 8.

Along with water, plant roots absorb both macro- and micro-nutrients for normal growth. To optimize absorption of nutrients from the soil, an adequate concentration gradient should be maintained between the root surface and soil solution. The process of nutrient absorption consists of both active and passive ion absorption. The gradient of the mineral concentrations in the cell sap is maintained by the ascent of sap from the root to the foliage. Nutrient absorption by the root system depends on nutrient concentrations in soil water.

Nutrient content translocated through root is related to the photosynthetic activity of leaves because several essential nutrients are directly or indirectly related to photosynthesis and respiration. For example, nitrogen forms the main component of proteins which in turn is the main constituent of protoplasm, chloroplasts and mitochondria. Phosphorus is an energy-rich compound directly related to the metabolic processes. Similarly, potassium regulates the opening and closure of the stomata, promoting carbon dioxide diffusion in the green tissues. Nutrient deficiency disrupts the normal growth and development of the plant showing hunger signs such as yellowish leaves, a symptom of nitrogen deficiency, or a purplish pigmentation of the culm and leaves due to phosphate deficiency. Nutritional disorders of some elements causes visible symptoms in sorghum (Gallagher *et al.*, 1975; Kawasaki and Moritsugu, 1979; Clark, 1982). Aluminum toxicity reduces root growth (Clark, 1982). The mineral nutrition of sorghum was reviewed by Myers and Asher (1982).

Climatic factors play an important role in the uptake of nutrients. In a low rainfall area where crop population is sparse, the response to fertilizer is less. For crops grown predominantly on stored moisture, progressive drying of soil from the surface downwards starves the upper part of the soil of mineral nutrients (Myers and Asher, 1982).

Nitrogen Nutrition

Mirhadi and Kobayashi (1979) studied the effect of different levels of nitrogen application on growth, grain yield and chemical constituents of grain sorghum. Nitrogen content was highest in green leaf blades, followed by stems, roots, dead leaves and threshed head parts. This order was affected by nitrogen level in the medium. They found that nitrogen content in grain increased with an increase in nitrogen in the medium. They also observed that the amount of nitrogen required for the highest yields of crude protein in the grain was very high, suggesting the need for nitrogen fertilization. They also showed that the total nitrogen content per plant unit, dry weight of each plant part was remarkably higher at early growth stages, but decreased rapidly towards the soft dough stage. At this stage, there was no correlation between nitrogen content and the age of the plant. Nitrogen absorbed by the plant was distributed mainly in the stem and leaf blades during the vegetative stage, but was gradually translocated to the head for the development of grain. Nitrogen uptake of the plant was reported to be quite similar to that of fresh weight of plant; the total nitrogen in the plant was observed to be highest

at the hard dough stage. They found 2 peaks of absorption of nitrogen: at vegetative stage for the rapid development of plant parts and the reproductive stage, and the development of grain.

Nitrogen and phosphorus uptake

Myers (1980) observed a relationship between root development and nutrient uptake in sorghum. Root development was rapid during the early crop growth cycle, reaching a peak dry weight at the mid-elongation phase, declining thereafter. Nitrogen and phosphorus levels were highest in roots when applied during the mid-elongation phase, but declined at later stages.

Sometimes, even though the surface soil is nutrient rich, it is too dry for roots to take up nutrient. Nutrient accumulation occurs at depth and it has been reported by Lavy and Eastin (1969) that substantial amount of ^{32}P occurred at depths of 30 and 60 cm. Smith and Myers (1978) found that much of the phosphorus and nitrogen uptake in water stressed dry land sorghum during grainfilling took place from the subsoil. This cautions the assessment of nutrient status of the sub-soil for a correct interpretation of the results of the field experiment. Myers and Asher (1982) and Cowie (1973) made a detailed study of the effect of N stress on N distribution in cultivar RS 610 in solution culture. They showed that under favorable growing conditions in the field, very little N remained within the root zone by anthesis when the fertilizer rate was (1/2 kg/ha). In the highest N treatment (336 kg N/ha), there was sufficient N in the soil during grainfilling. Significant net losses of N were observed from N-stressed sorghum after flowering.

ROOT SYSTEMS STUDY TECHNIQUES

Brick chamber technique

A brick chamber method was developed at ICRISAT (unpublished) to study sorghum root development. The chamber (65 cm long, 50 cm wide, and 150 cm deep) with 3 cemented sides, and a front made of brick and smeared with mud. The chambers were gradually filled with soil (red or black) followed by continuous addition of water, and continuous packing of the soil with bamboo sticks for uniform compaction. After filling with soil the brick chambers were exposed to rains throughout the rainy season to ensure natural compaction before being used. Once the desired amount of growth had occurred, the bricks of the front wall were dismantled brick by brick from the top, and the roots were washed slowly with water by using a hose pipe. The whole root system can then be exposed, and the pattern of distribution of roots in different soil layers can be investigated.

Though the soil compaction in brick chambers did not simulate the bulk density in the field, nevertheless a comparative study of the growth and development of whole plant root system of different selected genotypes was possible in the chambers.

General patterns of root development (genotypic comparison)

Improvement in root development and function seems to be reflected in final crop yields. Under periods of water stress, plants must proliferate roots in unexploited areas of the soil. The plant's ability to endure water stress is governed mainly by the rate of root proliferation and establishment during periods of

favorable moisture. Deep root systems also help in the efficient uptake of plant nutrients in the soil.

Laboratory study (Petri-plate culture)

It is important to know whether different genotypes show variations in the growth of radicle and plumule and how these variations are reflected in the final expression of the root systems. To obtain basic information about the growth of radicle and absorptive hair, different genotypes were grown in Petri dishes. Studies on CSH1, a non-heterotic hybrid, and 22E, a heterotic hybrid and their parents indicated that radicle and plumule lengths, and number of absorptive hairs were higher in 22E, a hybrid that showed heterosis in these parameters. A comparative study of radicle lengths of sorghum grown in Petri dishes for 5 days and in wooden trays indicated that a positive correlation existed between the 2 treatments.

Studies in pots and wooden trays

Studies on 36 genotypes in wooden trays for 20 days showed that the root system in different genotypes varied widely (range 0.044-0.15 gm/plant). Studies on the root system of another set of 48 genotypes on the 30th day indicate that there was much variation in their root systems, specially in total length, length of root canopy and average length of main adventitious roots. The total root length of the genotypes range between 106-191 cm, the majority of being between 104-174 cm. Thirty genotypes belonging to different taxonomic groups studied in pot culture also showed much variability in the components of their root system on the 30th day.

Root studies in polythene bags

To understand whether genotypic variability exists in the root system at the seedling stage, a set of 62 sorghum genotypes were grown in polythene bags (30 cm long and 10 cm diameter) in a greenhouse; 400 ml water were supplied in each bag containing 3 plants. Roots and shoots were washed 15 days after emergence. Genotypes showed significant variability for seedling vigor measured in terms of seedling height, seedling dry weight and also root dry weight.

CSH1, 22E and their parents (pot culture)

A comparative study on root systems of CSH1, 22E and their parents at 15, 30 and 45 days revealed that CSH1 showed much lower values compared to its parents in most major characteristics, but in total root length and dry weight of roots/shoot ratio, CSH1 exceeded its parents. In 22E, total root length and dry weight of root/shoot were much lower than those of its parents. The limitations of root studies in pot experiments are well known. Genotypic variability can, of course, be studied only between 15-30 days in the pot culture experiments.

Brick chamber method

The brick chamber method attempted to study root development of CSH1 and 22E, an unreleased hybrid. In 3 sets of different brick chambers, root and shoot samples were collected at 45, 60 and 75 days by dismantling the chambers. Measurements were made on the number, length and weight of roots and shoots. CSH1 and 22E were sown in brick chambers lined with polythene at different levels to observe the rate of root growth up to the stage of physiological maturity. The rate of root growth in 22E was higher than CSH1 in the early stages but at 75 days, CSH1 had more roots than 22E. It was also observed that the new flush

of roots coincided with the boot stage (60 days in 22E and 75 days in CSH1).

At 60 days, the total number of main adventitious roots produced per plant was greater in 22E than in CSH1 (37 and 27 respectively). At 75 days, they were greater in CSH1 than in 22E (72 and 41 respectively). Similarly, at 60 days the total root length of the main adventitious roots was higher than in CSH1 (1934 and 1420 cm respectively) but at 75 days, CSH1 exceeded 22E (1934 and 1420 cm respectively). However, the average length of each main root at all stages was greater in 22E than CSH1 (35 and 27 cm respectively at 75 days). The average dry weight of roots per plant at all stages was greater in 22E than in CSH1 (25 and 25 g respectively at 75 days). Root/shoot ratio at all stages was greater in 22E than in CSH1 (0.48 and 0.35 respectively at 75 days). At harvest, most adventitious roots had decayed and only the top crown roots were present in the upper layer of the soil. A comparative study of the growth and development of the underground and above ground parts of the 2 hybrids (CSH1 and 22E) and their parents demonstrated that hybrids grew faster than their parents, but showed a higher level of heterosis than its parents when compared to the CSH1 (ICRISAT, 1977).

Field study

CSH1, 22E and their parents were grown in alfisol during the post-rainy season of 1976 under irrigated conditions in the field. Whole plants along with roots were collected at different stages, i.e., panicle initiation, boot stage and flowering stage (50 X 50 cm²) were dug to a depth of 75 cm and filled with water, and left overnight to soften the soil. On the next day, roots were washed carefully in different layers of the soil.

It was observed in both cultivars that at panicle initiation under irrigated conditions new roots formed a spreading canopy horizontally in a network pattern within 10 cm depth of the soil. At this stage some collar roots had also developed.

At boot stage, the main adventitious roots grew laterally up to 25 cm, and produced a profuse network of lateral roots. In CSH1, the crown roots had produced lateral roots whereas in 22E they had sent out profuse lateral roots in a network pattern. The main adventitious roots got distorted and some of the roots were found dried out. In both cultivars the main adventitious roots which were developed in the upper 10 cm layer at panicle initiation were found to decay and lose their activity as shown by the lack of root hair. The seminal roots were found to lose their root hair at this stage. In all the genotypes, a new flush of adventitious roots was found to develop at boot stage.

At the flowering stage, in 22E, the adventitious roots that were formed at panicle initiation were present, but some of these were inactive and dried up with the loss of root hair. CSH1, however had persistent profuse root systems when compared to that in 22E. The zone of maximum root hair was limited within 45-50 cm in CSH1 and 35-40 cm in 22E. The crown roots that had already formed were found to produce extensive root hairs and played a predominant role in the root system both in CSH1 and 22E. Maximum depth of root penetration was 70 cm in CSH1 and 50 cm in 22E.

Parents of CSH1 and 22E showed only slight deviation from their hybrid vigor. In general, the hybrids (CSH1 and 22E) produced a higher amount of root weight

and root/shoot ratio when compared to their parents. Root/shoot ratio decreased from panicle initiation to boot and flowering stage. Under field conditions, the hybrid 22E was superior (heterosis) over its parents but this was not pronounced in CSH1 (Figs. 6.11-6.14).

Effect of soil types on root growth in brick chambers

Twelve chambers were filled with red soil and an equal number filled with black soil. Seeds were sown in 2 rows 30 cm apart with a space of 10 cm between plants. Ten days after emergence, the surface of the soil was covered with a 4 cm thick layer of fine sand which was then covered with a dark polythylene sheet layered with gravel to prevent evaporation losses from the soil surface. The plants were allowed to grow on the stored moisture. At 10 days intervals, two chambers of each soil type were dismantled to study the root system from 30 days after emergence until maturity.

Developmental stages

Grain sorghum (CSH8) did not show significant difference in the attainment of different physiological stages in red and black soils (Table 6.1). In general, vegetative stages and early reproductive stages (1 to 5) were earlier in red soil than in black soil, but grain development stages were late only by 2 days. As the hybrid was grown in stored moisture and no further irrigation was provided, the physiological stages were somewhat delayed in red soil owing to water stress. The growth rate of the above ground parts in general was less in red soil compared to that in black soil (Figs. 6.15, 6.16). This observation was confirmed by measuring leaf water potential which was lower in red soils than in black soil (Fig. 6.17). Measurements made were maximum root penetration in the soil, number of roots (and root dry weight) at different depths, the leaf area and length of stem. The tops were partitioned into leaves, stems and panicles, and were measured. The root biomass (Figs. 6.18 - 6.20) increased at a slow rate up to 30 days (early vegetative stage), but increased rapidly up to 60 days in black soil and 70 days in red soil, not increasing appreciably thereafter. By that time, CSH8 passed the half-bloom stage. The total dry matter at all stages though not significant, was less in black soil than in red soil.

Table 6.1 Physiological stages of development of grain sorghum in relation to date and days after emergence (in brick chamber).

Stage	No. Stages	Red soil (Days)	Black soil
0	Emergence	0	0
1	3 leaf	3	3
2	5 leaf	8	10
3	Growing point differentiation	-	-
4	Flag leaf visible	42	45
5	Boot stage	48	50
6	Half bloom	60	60
7	Soft dough	92	90
8	Hard dough	98	96
9	Physiological maturity	104	102

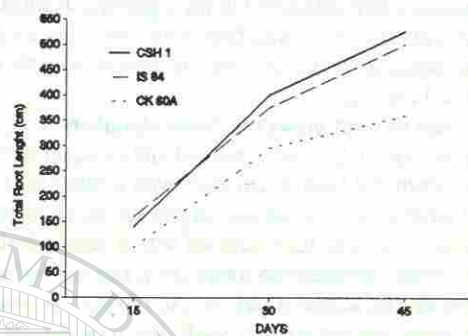


Fig. 6.11 Total root length in CSH1, an Indian hybrid and its parents at different stages.

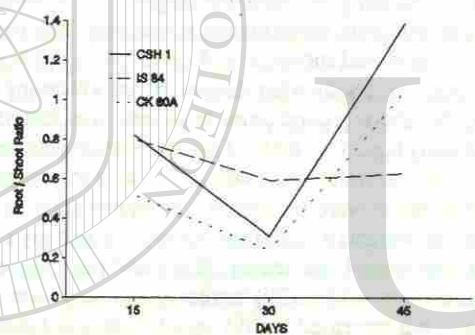


Fig. 6.12 Root/Shoot ratio in CSH 1 hybrid and its parents at different stages.

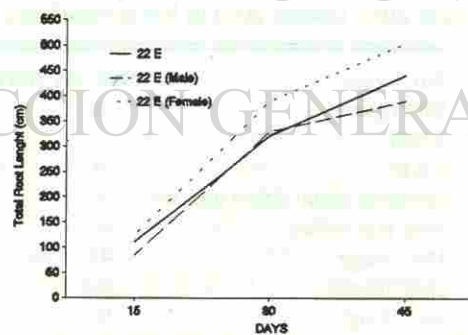


Fig. 6.13 Total root length in 22 E hybrid and its parents at different stages.

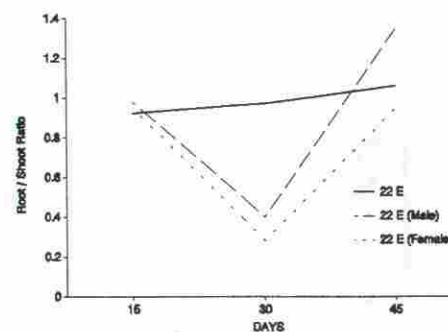


Fig. 6.14 Root/shoot ratio in 22 E, a hybrid and its parents at different stages.

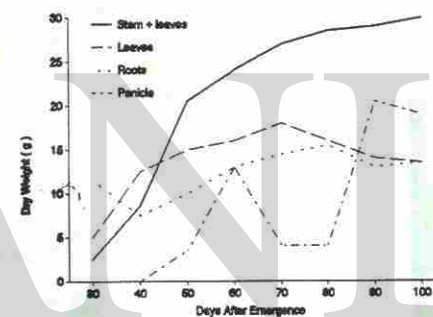


Fig. 6.15 Dry matter distribution at different stages of growth of CSH8 in red soil, post-rainy season, 1977.

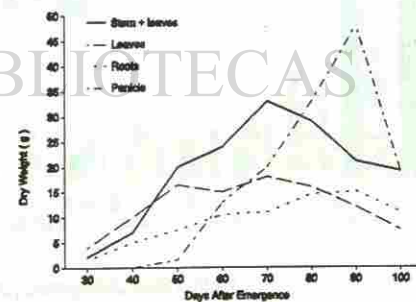


Fig. 6.16 Dry matter distribution at different stages of growth of CSH8 in red soil, post-rainy season, 1977.

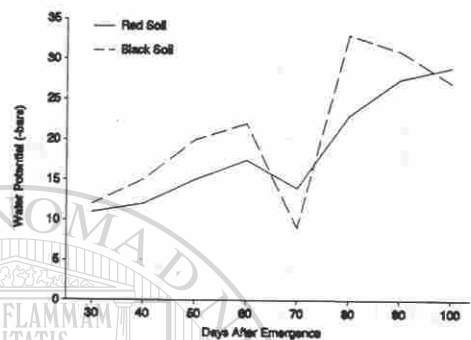


Fig. 6.17 Gradients of water potential of leaf in brick chambers in alfisol and vertisol at different stages of growth of CSH8, post-rainy season, 1977.

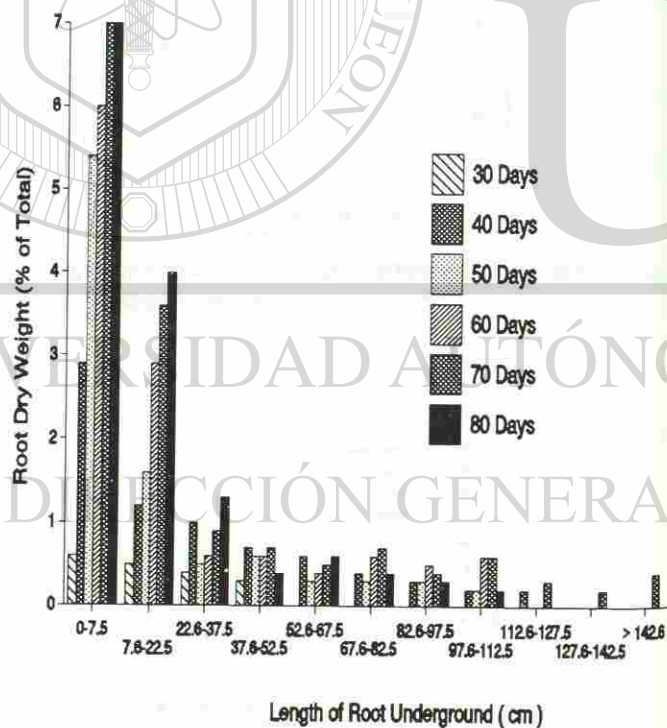


Fig. 6.18 Distribution of root bio-mass at different layers of black soil at different stages of growth of CSH8, an Indian hybrid, 1977.

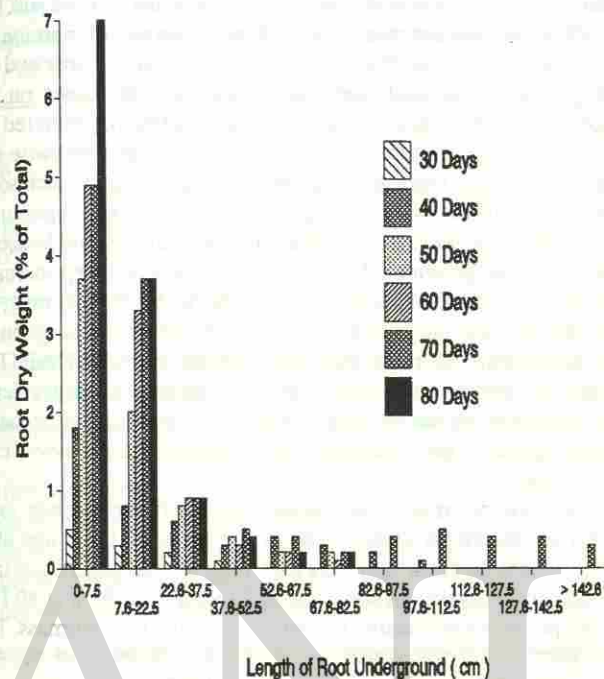


Fig. 6.19 Distribution of root bio-mass at different layers of red soil at different stages of growth of CSH8, an Indian hybrid, post-rainy season 1977.

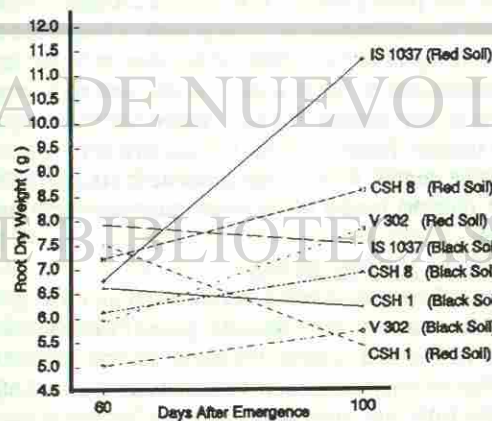


Fig. 6.20 Accumulation of dry weight in roots at different stages of growth in black and red soils.

The penetration of roots was also less in black soil than in red soil. Therefore the growth of the root system was more profuse in the red than in the black soil. This might be because of the fewer number of large size pores and the lesser water holding capacity of black soil. As the plants were grown on the same moisture, the red soil with its lesser water holding capacity promoted the downward proliferation of water to the root systems. There was a stepwise increase in leaf water potentials with the age of the crop both in red and black soils, though it was always higher in red soil indicating that more stress was experienced in black soil (at 70 and 100 DAE the brick chamber received rainfall and hence there was a sudden fall of water potential; Fig. 6.17). There was a sharp increase in root depth up to 40 DAE in red soil and 50 days in black soil. By this time, the hybrid had crossed the flag leaf stage in red soil and reached boot stage in black soil (Table 6.1). Senescence of roots increased rapidly after 70 DAE. During the grainfilling period, the main function of the root seemed to be restricted to that of support. The maximum penetration of root at the upper layer of the soil in the brick chamber simulated the field condition reported by other researchers (Jain and Weaver, 1924).

Most of the root dry matter was concentrated in the surface layers (0 to 22.5 cm). This accounted for 70% of the dry matter at 30 DAE and almost 80% at 80 DAE in red soil. In black soil, the percentage of root dry matter in this layer was even larger; total dry weight was 80% at 30 DAE and 90% at 80 DAE. The roots in the deeper layers accounted for very little of the root biomass. The findings in brick chambers corroborated with the findings of Stone *et al.* (1973), Blomworth *et al.* (1958) and Nakayama and van Bavel (1963). Dry matter accumulation followed a similar pattern in red and black soils. Root dry matter started declining after 80 DAE in red soil and 90 DAE in black soil (Fig. 6.20) by which time the hybrid had almost reached soft dough stage.

The depth to which the roots penetrate and their distribution in different horizons directly affect the plant's ability to withstand drought. Soil scientists at ICRISAT tried to study the differences in root growth in black and red soils. A machine collected core samples of 7.6 cm diameter taken at 15 cm increments in red soils and 30 cm increments in black soils. The soil and root samples were washed to separate roots, and measurements consisted of the composite length of roots taken in each sample. Table 6.2 gives the data as a percentage of the total root lengths by respective depths. Most of the roots were present in the top layer of the soil in the field, thus the results of the brick chamber studies seem to be in line with field observations.

Coordination of top growth and root growth

There seemed to be a linear relationship between top and root growth (Petersell, 1927) during vegetative and midreproductive phase (Table 6.3) but between 60-70 days the top growth seemed to be stable while the root growth declined as the roots senesced. This finding was similar to that obtained by Kaigama *et al.* (1977), who found that from the sixth developmental growth stage, the above ground growth was stable, while root depth was stable in the field from stage 5 to stage 6. Thereafter, there was senescence in the root system which was not taken into account by the coring technique (Kaigama *et al.* 1977). The extraction

Table 6.2 Depth and distribution of roots of sorghum grown on black and red soils-expressed in percentage by depth increments, Hyderabad 1975 (ICRISAT, 1977).

Soil	Depths (cm) at which samples were taken					
	0-30	30-60	60-90	90-120	120-150	150-180
Black soil	49.4	18.1	15.4	11.4	3.5	2.2
Red soil	35.4	13.5	19.4	15.9	14.1	1.7

Table 6.3 Relationship between root and shoot dry weight in red and black soils at different stages of growth (correlation, brick chamber).

	1	2	3	4	5
1 Days after emergence	1				
2 Root dry wt./plant (g) red soil	0.93**	1			
3 Root dry wt./plant (g) black soil	0.72**	0.76**	1		
4 Shoot dry wt./plant (g) red soil	0.92**	0.90**	0.82**	1	
5 Shoot dry wt./plant (g) black soil	0.94**	0.90**	0.90**	0.94**	1

of roots from the soil included both live and senesced roots. As a result, there was a downward trend of root depth during the late grainfilling phase. Therefore, while shoot dry weight increased, the death of older roots might not be fully compensated by new growth. High yielding cereals have been reported to be accompanied by a progressive decrease in the weight of roots (Evans and Dunstone, 1970). To maintain the source-sink relationship, the coordination between root and shoot growth is essential (Brouwer, 1965). This relationship is reported to alter during the later stages of development due to changes in the partitioning of dry matter between roots and shoots under different environmental factors (Nielsen and Cunningham, 1964; Brouwer, 1965; Brouwer and De Wit, 1969; Russell, 1977). González-Rodríguez (1989) made a quantitative estimation of root development.

The increase in plant dry matter was slow during the early stages and increased rapidly from 30 days onwards. The above ground portion formed the bulk of the dry weight. At maturity, the stem contributed only 16% to the total dry weight in the red soil and 10% in the black soil. The root-shoot ratio was higher in red soil (0.19) than in black soil (0.11). The low water holding capacity of the red soil enables better plant growth by efficient usage of stored moisture. This might be the reason for the higher growth rates in the red soil. Owing to some stress in red soil, the normal growth of panicle was checked and the panicle was malformed. Leaf area index (LAI) increased rapidly to a maximum at 50 DAE in both red and black soil. Thus, maximum photosynthetic efficiency is reached around boot stage. In the black soil, CSH8 attained a maximum of 5.3 LAI compared 4.9 LAI

in the red soil.

The study clearly shows that both shoot and root dry weight correlate positively with the age of the crop. Root and shoot also showed significant positive associations between themselves in both soils (Table 6.3). Root dry weight increased significantly with the age of the crop and was much larger in red soil. Significant positive correlations were observed between root and shoot dry weights and the age of the crop for both soils, although the relationship of root dry weight was weaker than shoot dry weight. Shoot dry weight also showed a strong positive correlation with root weight in red soil and black soil.

Responses of some cultivars showing different levels of drought tolerance in black and red soils

Four sorghum cultivars IS 1037 (drought-tolerant type), CSH8 (avoidant), CSH1 (intermediate), and V302 (susceptible) were grown in brick chambers under irrigated conditions to find out differences in root growth. The brick chambers were dismantled at 2 stages, 65 DAE and 95 DAE. The root biomass is given in Table 6.4.

Table 6.4 Dry weight of roots (g) in plant of some sorghum cultivars in black and red soils

Genotype	Black soil		Red soil	
	65 days	95 days	65 days	95 days
IS 1037	6.88	11.41	7.95	7.62
CSH8	7.36	8.58	5.99	6.90
CSH1	7.47	5.39	6.65	6.15
V302	5.90	7.76	5.10	5.73

It is possible to differentiate the genotypes with respect to root growth with the use of the brick chamber technique. In red soil, IS 1037 and CSH8 which showed drought resistance under field conditions also showed maximum root biomass. Under irrigated condition, higher water holding capacity in the black soil with less water holding capacity of the red soil might have encouraged the root growth in the deeper layers. Thus, the hypothesis that the roots of drought-resistant cultivars are longer than the more susceptible ones could be confirmed using the brick chamber technique.

Usefulness of the brick chamber technique

Despite its drawbacks, the brick chamber technique may be used for the following specific studies:

1. Development of the root system, the growth pattern and proliferation of individual roots with the age of the crop and their distribution of different levels of the soil.
2. Correlation of root and shoot growth to assess the stage at which the root system (a) shows maximum efficiency and (b) starts to senescence.

3. Finding genotypic differences in root growth for subsequent correlation with drought and yield responses.
4. Root competition in intercropping and to suggest ideal crop mix for diverse environments.
5. Nodulation of pigeonpea intercropped with sorghum.
6. Finding out the responses of cultivars to different levels and methods of applying fertilisers.
7. Finding differences in root growth of cultivars induced by changes in soil texture, moisture and fertility.

GENERAL COMMENTS

Although attempts have been made to study the root systems in sorghum, very little progress has been made. The main reason for this is that efficient techniques to study root systems in the field are not available. Another is that roots - unlike other plant parts - are inaccessible to direct observation without elaborate excavation. Much of our knowledge of root development is based upon laboratory cultured seedlings in rhizotron. As roots play an important role in the uptake of water and nutrients, crop productivity is largely dependent on an efficient root system. Due to the limitation in conducting root studies, it is difficult to correlate crop productivity with the efficiency of root systems. The adaptability of a crop cannot be judged in proper perspective if we neglect the performance of its root system. Root estimation with the help of soil cores cannot give a clear picture of the entire root system in the field, and some simple techniques need to be developed to study them. Genetic variability in the root system, which is an essential prerequisite for genetic improvement, has been reported by different researchers. Studies also report a relationship between root depth and drought resistance. These need to be confirmed by further research.

As a number of research studies indicated that more than 80% of the total root mass was located in the upper 20-30 cm soil layer, techniques need to be developed to assess root mass from the upper layer of soil to enable the categorization of sorghum genotypes on the basis of this trait. We also need to identify genotypes which have greater root mass in the upper layer and which also have a large number of roots at a deeper soil level. The genotype with this "root ideotype" may be adaptable to adverse soil conditions. We need to study whether seedling root system is in any way related to the performance of the adult system. Therefore, genotypes need to be evaluated for efficient root systems at the seedling stage both

under normal and stress situations (water/nutrient). The hope is to correlate the resistance at the seedling stage with resistance at the adult stage. This may be assessed in a long glass tube, a PVC cylinder or a brick chamber, and may help us to compare the total root system of different genotypes.

Root studies in brick chambers have shown good correlation with that in the field in terms of pattern of root distribution in the soil as well as the drought resistant nature of some sorghum genotypes. Root elongation in tube culture or

cylinder could be correlated with the extension of root into deeper soil in the field. We need to verify this assumption. If this is successful, a large number of genotypes could be evaluated at the seedling stage. However, we need to direct our research efforts on root studies to select genotypes adaptable to adverse climatic and edaphic environments of the semiarid tropics. No studies have yet been made on the contribution and function of different members of the root system (taproot, seminal, adventitious and nodal, in relation to crop growth. We need to explore if correlations exist between certain anatomical characteristics like intercellular pericycle lignification and silica crystals, and biotic (e.g., *Striga*) or abiotic stresses (e.g., drought).



ROLE OF CLIMATIC FACTORS ON SORGHUM GROWTH

7

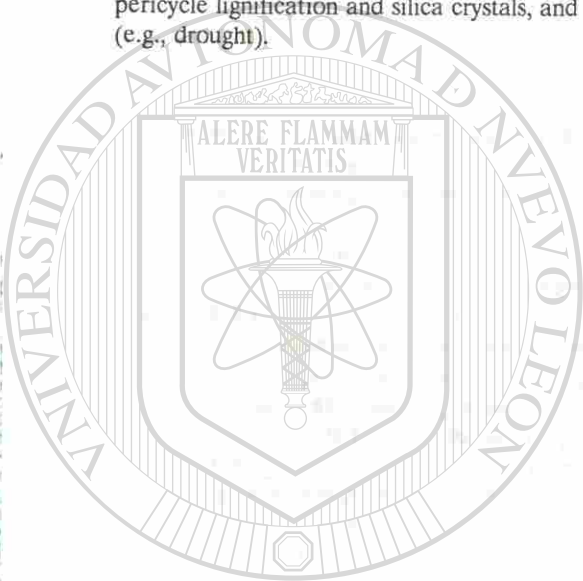
INTRODUCTION

Climate plays an important role in determining the growth and development of a crop. The expression of phenotypic traits is the result of interactions of genotypes and the environment. The productivity of the crop is the yield of plants expressed as a unit of some factor that limits production (Elston, 1980). At different stages of crop development, several physical and biotic factors may operate simultaneously in limiting plant growth, but productivity under different environment is determined by several plant processes like transpiration, water use efficiency and assimilate partitioning (Fisher & Turner, 1978). These are in turn highly controlled by the environment. The growth of a crop through its various developmental phases is guided by different environmental components. Germination and emergence are highly influenced by temperature and soil humidity and density, while canopy development, very important for the interception of light for efficient photosynthesis, is influenced by the photosensitive nature of the genotype. Photosensitive cultivars continue to maintain uninterrupted leaf production without producing any effective panicle unless a particular day length is reached. Panicle initiation is highly influenced by the day length.

Of the different environmental factors which affect the sorghum crop, soil and atmospheric environments are the most important. These are further influenced by biotic factors and crop management. It is therefore necessary to understand the environmental parameters and their influence on crop growth. Large diversity and variability of environments in different sorghum-growing regions affect sorghum production. The environment influences yield by directly interacting with the physiological processes of sorghum production and indirectly through diseases and insects. This chapter discusses macro- and micro-climates and their role in crop growth.

SORGHUM GROWING REGIONS AND THE ENVIRONMENT

Sorghum is grown in the semiarid tropics (SAT) right from sealevel to elevations of 3000 m, including high, low and variable rainfall areas, as well as different seasons of the year. The sorghum crop is widely adaptable to varying soil and environmental conditions. Miller (1982) proposed that sorghum breeders should



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have good knowledge of the climatic environment in which they work, and they should develop highyielding and more stable varieties for that zone by obtaining appropriate collections from diverse climates and recombining them into more widely adapted improved types. He also stated that sorghum has moved from Ethiopia to USA, Argentina, Venezuela, Central America, Australia, India and several areas of Africa. The crop is grown between the tropics of Capricorn and Cancer (23.5° N and S Latitude). The main area of diversity in both wild and cultivated sorghum is in the northeast quadrant of Africa which is claimed as the origin.

Doggett (1970) concluded that the great diversity in *Sorghum bicolor* existing in the ecological habitats of northeast Africa was due to disruptive selection, isolation and recombination. Although sorghum is grown in some temperate regions, it is one of the major crops in the semiarid tropical countries of the world where the crop has to face adverse climatic conditions during its growth period. Based on the data of average production of sorghum during 1974-78 in different countries, Von Oppen and Ryan (1981) analyzed sorghum production in different regions in SAT. According to them, India produces 34% to the crop grown in SAT, and is the largest sorghum producing country in the world. The other major sorghum producing countries in Asia are Pakistan, China and Thailand. In the Americas, México and Argentina together produce 34% of the crop grown in SAT. The major sorghum growing countries in west Africa are Ghana, Niger, Nigeria, Upper Volta and Mali contributing 15% of the production in the SAT. Ethiopia, Kenya, Sudan, Tanzania, Malawi, Mozambique, Zimbabwe and Zambia are the major producers in eastern and southern Africa; while Saudi Arabia and Yemen contribute only 3% of the crop grown in the SAT. Von Oppen and Ryan (1981) defined core sorghum growing regions contributing at least 20% of the share in the SAT, and on this basis Nigeria, Ethiopia, Sudan, Malawi and Mozambique represent the core production areas.

In India, rainy season sorghum areas extend from 9°N (Madurai in Tamil Nadu) to 25°N (Hamirpur, Himachal Pradesh) while the post-rainy season sorghum growing areas lie within the narrow belt of 14°N (Nellore, Andhra Pradesh) to 21°N (Dhule, Maharashtra). Over 99% of sorghum in India is produced in the SAT areas (Tables 7.1 and 7.2).

With its versatile adaptability and its use as a food and feed, sorghum is grown in the seasonality dry tropical climates spread over 4 continents and 48 countries. They are characterized by having mean annual temperatures greater than 18°C and rainfall exceeding evapotranspiration for only 2 to 4.5 months in the dry SAT and for 4.5 to 7 months in the wet/dry SAT. The coefficient of variability of rainfall in SAT is 20 to 30% (Higgins, 1978).

The several constraints to sorghum productivity in the SAT include intense rainfall interspersed with drought, a short but variable rainy season, high rates of evapotranspiration in the growing season and low infiltration capacity of the soil. These diverse environmental conditions have a direct impact on the growth and development of sorghum. Miller (1982) identified vast areas in southern Russia, northern China, South America and some areas in South Africa and Australia where sorghum has potential for expansion.

Table 7.1 Highest and lowest air temperature recorded in the rainy season sorghum growing season at selected locations in semiarid India (Sivakumar & Virmani, 1980).

Location	Jun	July	Aug	Sep	Oct	Nov
Akola	42.2	36.2	31.4	35.0	35.6	33.6
Hyderabad	22.5	21.8	21.7	21.1	14.7	10.6
Indore	39.9	34.0	33.0	32.8	33.3	31.5
Jhansi	21.2	21.0	20.9	20.3	15.8	11.8
	40.0	34.1	31.5	32.6	33.2	31.2
	21.4	21.0	20.4	18.9	13.0	8.2
	44.9	39.6	35.5	35.6	36.0	33.4
	23.8	23.1	22.7	21.6	14.7	8.8

Table 7.2 Highest and lowest air temperature recorded during the post rainy sorghum growing season at selected locations in semiarid India (Sivakumar & Virmani 1980).

Location	Oct	Nov	Dec	Jan	Feb	Mar
Bijapur	33.6	31.8	31.4	32.7	35.8	38.5
Gulbarga	17.0	12.9	11.1	12.0	14.1	17.3
Sholapur	34.4	32.8	31.5	32.7	36.1	39.4
Ahmednagar	16.8	12.9	10.5	11.7	14.3	17.4
	34.7	32.2	31.9	33.3	36.4	39.7
	16.6	12.9	10.7	11.3	13.1	16.7
	33.5	32.2	31.1	32.0	34.4	38.5
	14.5	10.5	8.0	8.0	9.6	13.0

Sivakumar and Virmani (1982) briefly describe the salient features of the environment in sorghum growing areas of Africa and India:

Radiation

Solar radiation guides photosynthesis in the production of biomass. The amount of dry matter produced by plants depends, to large extent, on the interception of the incoming solar radiation by the crop canopy. The total solar radiation in SAT Africa ranges from 400-500 cal/cm²/day with the highest solar radiation in the northern and southern boundaries of semiarid Africa. The average global solar radiation during the rainy season varies from 400 to 450 cal/cm²/day while in the post-rainy season it is reduced by 10-40 cal/cm²/day.

Temperature

The average maximum temperature varies from 35°C in northern Upper Volta, Niger and Sudan to 22°C in the Ethiopia highlands. The average maximum

temperature in Kenya and Tanzania ranges from 25-30°C while the minimum ranges from 10-23°C.

In India, sorghum is grown in the rainy and post-rainy seasons. The average temperature in the rainy season varies from 31°C (in the early growing season) to 28°C (in November). In the post-rainy season, the average mean temperature ranges from 22 to 29°C. Therefore, the maximum temperature variation during the rainy season is not significant, but the minimum temperature decreases from 25°C to 20°C, by the time the crop reaches physiological maturity (August-September). In the post-rainy season, the maximum temperature rises from 30°C in October to 35°C by March and 42°C by April. The small change in diurnal temperature range in the rainy season promotes good vegetative growth and grainfilling. In the post-rainy season, the large diurnal range in temperature has a direct impact on the growth of sorghum (Peacock, 1982). Among sorghum-growing areas in India, the maximum temperature can reach as high as 45°C at Jhansi, while the temperature could go down as low as 8°C in November as in Indore. In the post-rainy season, the maximum temperature could reach as high as 40°C, while a minimum temperature of 8°C is not uncommon. The highest and lowest temperature in SAT India are given in (Tables 7.1, 7.2 and 7.3).

Table 7.3 Seasonal average weather data and photoperiod at Hyderabad (17.5°N) during different phases of crop growth: 30 genotypes including hybrids and parents.

Elements	GS1				GS2				GS3		
	K	DR	R	JR	K	DR	R	JR	K	DR	JR
Max. Temp. °C	31.1	28.3	31.4	27.4	30.0	29.7	32.2	32.4	29.1	28.8	36.1
Min. Temp. °C	22.6	15.3	21.6	12.2	22.2	13.5	19.6	14.6	22.1	14.7	19.2
Avg. Temp. °C	26.9	21.8	26.5	19.8	26.1	21.6	25.9	23.5	25.6	21.6	27.7
Sunshine hr/day	2.8	9.4	9.6	10.0	4.1	10.3	10.4	10.7	4.3	10.4	10.1
Photoper. hr/day	13.1	11.1	12.0	11.3	12.9	11.2	11.5	11.7	12.5	11.5	12.3
Avg. Rel. Hum. %	71	66	64	57	80	49	57	45	79	51	35

K = 14th June 1976 planting; DR = 1st December 1976 planting;
R = 11th September 1976 planting; JR = 19th January 1976 planting.

Rainfall

As for any other crop, the amount and variability of rainfall has a pronounced effect on yield. The west African region of Ghana, Upper Volta, Niger and Nigeria receive an annual rainfall between 800 and 1600 mm, while the region receiving between 1000 and 1600 mm rainfall is classified as the Sudano-Guinean zone. The early season in this region lasts 4 to 5 months. The eastern Ethiopian highlands receive a rainfall of 1200-1300 mm on the western side of the high plateau, while the eastern valley receives less. Rainfall in the Kenyan highlands is 1200-1500 mm while the western side is more dry rainfall in north and central Tanzania is low. south-western Tanzania receives more rainfall. Rainfall in southern Africa is fair

great. Mozambique, Malawi, Zimbabwe and Zambia in southern Africa receive rainfall ranging from 400 to 1600 mm.

The rainfall isohyets in sorghum-growing regions in India ranges from 700 to 1400 mm. Most of the core sorghum growing areas in the rainy season are located between 800 and 1000 mm rainfall isohyets, while the core post-rainy season sorghum growing regions fall in the belt with low and uncertain rainfall up to 800 mm.

TEMPERATURE

Temperature influences sorghum yield by directly affecting the physiological processes involved in grain production and indirectly through diseases and insects.

The effect of temperature on growth and development and physiological processes is fairly known. The response of temperature varies with the crop and also among varieties. The physiological processes in cultivated crop plants are controlled by a wide range of temperatures. Leopold and Kriedmann (1975) indicated that the temperature extremes within a biological range exert selective pressure for survival or elimination of individuals within a species. Thus, in order that the tropically-adapted types have a selective advantage with low base temperature, they must have come from an area which does not experience freezing temperatures. Base temperature is the temperature at which 50% of the seeds fail to germinate in 18 days (Miller, 1982). The plants developed in these regions would not be subjected to frost early in the growth period and would not be eliminated from selection as they would be able to germinate with the onset of rain. This early establishment could force selection for pest resistance. On the other hand, the genotypes which were developed at high elevations or in areas where frost was prevalent early in the season, survived only if they did not germinate too early when frost occurrence was high.

The plants with high base temperatures become adapted to highland areas of Ethiopia and the great plains in the U.S. while plants with lower base temperatures are more adaptable to warmer nighttime environments of south Texas, Venezuela, the lowlands of Mexico, Australia, India and the lowlands of Ethiopia and Africa (Miller, 1982).

Arnold (1959) indicated that the base temperature for sorghum germination is 10.5°C. Thomas and Miller (1979) using the procedure of Gbur *et al.* (1979) have shown that the base temperature is not constant within the species, but may vary from 4.6°C to 16.5°C. Thomas (1980) established that lines and hybrids which were 'tropically adapted' had a lower base temperature than the lines designated as 'temperately adapted'. Hybrids exhibited lower base temperature than their inbred parents. Miller (1982) stated that sorghum has the major adaptation factors of height, duration of growth, response to photoperiod and sensitivity to temperature when exposed to genetic manipulation. In his opinion temperature, photoperiod, rainfall and the interactions of these climatic driving forces interact within the biological range and exert selective pressure among sorghum species to affect adaptation in a particular area. Miller (1982) has also suggested that

major variations exist within *Sorghum bicolor* for base temperature. These differences in response among plants indicate that by measuring temperature characteristics, there may be more effective ways of predetermining areas of geographical adaptation. This may allow the breeder to predict ranges of adaptation for a particular cultivar in an environment. Rao and Rana (1982) state that temperate crosses have become an integral part of all sorghum breeding programs in the world. The conversion approaches have received emphasis in the USA and India. In most temperate-tropical crosses, when plants are grown under tropical conditions, the early stages are dominant. The following are some examples of the effect of temperature on sorghum growth.

Air temperature

Temperature indicates the capacity to transfer heat by conduction. Clear skies promote maximum radiation during daytime and rapid loss of heat at night. This in turn brings about wide diurnal changes in the aerial environment. Mean temperature is generally calculated in the following way

$$\text{Mean Temp. } ^\circ\text{C} = \frac{\text{Max. Temp. } ^\circ\text{C} + \text{Min. Temp. } ^\circ\text{C}}{2}$$

The temperature quotient, Q_{10} used to assess the effect of temperature on the rates of growth and differentiation (Yoshida, 1981) can be worked out as follows

$$Q_{10} = \frac{\text{Rate at } (T+10)^\circ\text{C}}{\text{Rate at } T^\circ\text{C}}$$

where Q_{10} is the increase in the rate for every 10°C rise in temperature.

Aerial temperature has a significant effect on sorghum growth, i.e., on photosynthesis, respiration, leaf temperature, phenology and other yield components. The critical temperature for growth varies from one growth stage to another and depends on crop variety. The effect of temperature on sorghum growth has been demonstrated by different researchers (Eastin, 1972a and 1976; Sullivan *et al.*, 1977; Angus *et al.*, 1980).

Effects on photosynthesis and respiration

Photosynthesis shows a decline with an increase in temperature and is inactivated at excessively high temperatures, but respiration may not be affected similarly (Moss *et al.*, 1961). Metabolic efficiency appeared to diminish between 25°C and 40°C in sorghum (Eastin and Sullivan, 1974).

Effect on phenology

Chowdhury and Wardlaw (1978) observed a reduction in the grainfilling period from 42 to 18 days by increasing temperatures from $21/16$ to $33/28^\circ\text{C}$. This is interpreted that metabolic efficiency expressed in terms of grains (GS3) is appreciably reduced by higher temperatures. Castleberry (1973) reported that the most sensitive period to temperature is when floret differentiation occurred.

When planted on the same date at different locations at same latitude, crops of the same cultivar may differ considerably in rates of growth and development. Differences caused by location often are greater than differences among cultivars grown at one location. This suggests that with a narrow range of latitude, variations in temperature may be largely responsible for differences in maturity among sorghum cultivars planted on the same date (Fryer *et al.*, 1966).

Gibson *et al.* (1977) reported that the greatest temperature response occurred

in GS1. This growth stage is largely dependent upon production and expansion of 6 to 8 upper leaves (Schaffer *et al.*, 1979) which support grain filling. The most important yield-seed number is determined during this phase. Hence planting date has to be decided ensuring that temperature during GS2 is most favorable.

A probabilistic model to predict the duration of different growth stages has been put forward by Reddy (1984). Temperature is found to have a significant effect on phenology and duration of different phases is curvilinear. This study indicates that even a slight change in temperature (1.9°C) causes contrasting variations in the duration of growth stages of sorghum cultivars belonging to different taxonomic groups (Tables 7.4 and 7.5).

Table 7.4 Phenology of CSH1, in days and Heat Units (HU) with 10°C as base temperature (Reddy *et al.*, 1984).

Phenophase	Days			Heat Units (HU)		
	Mean	Max-Min (range)		Mean	Max-Min (range)	
1-GS1	23.6	29-20 (9)		665.9	1065-506 (559.6)	
2-GS2	34.0	41-25 (16)		944.8	1224-787 (436.6)	
3-GS3	33.4	40-25 (15)		956.7	1265-766 (499.8)	
4-1+2	58.3	69-50 (19)		1595.8	2290-1344 (946.2)	
5-1+2+3	91.8	102-79 (23)		2552.5	3425-2233 (1192.2)	

The classical heat unit of degree day requirement varies for different growth stages of sorghum (Table 7.4). Growing degree days which determine the summation of heat units over the growing period is estimated in the following way:

$$\text{Growing degree days (GDD)} = \frac{\text{Min } T^\circ\text{C} + \text{Max. } T^\circ\text{C}}{2} - \text{Base } T^\circ\text{C}$$

Temperature is substituted for the maximum temperature if the maximum is higher than the cutoff temperature. When the daily minimum temperature is lower than the base temperature, a sine curve is used to approximate diurnal change in temperature between maximum and minimum. The relationship between GDD and different growth stages was found to be highest with 38°C cut off temperature and base temperature of 7°C (Huda, 1982). The classical heat unit concept is accurate enough to predict phenological events (Quinby *et al.*, 1973; Reddy, 1984).

Effect of temperature on yield components

Higher temperature (day/night $33/28^\circ\text{C}$) from germination to panicle initiation reduced grain yields of sorghum, as did high temperature during the last part of panicle development on floret abortion (Downes, 1972). Eastin (1976) exposed sorghum cultivars to day/night temperatures of $29/17^\circ\text{C}$, $29/22^\circ\text{C}$, $29/27^\circ\text{C}$ and $34/22^\circ\text{C}$ from panicle initiation to bloom and showed that night temperature $2-3^\circ\text{C}$ above the optimum reduced yield by 25-33%. In sorghum, the rate of kernel development at higher temperature ($30/25^\circ\text{C}$) was greater than other cereals. In wheat, the rate of development of individual kernels was higher at

lower temperatures (21/16°C) than in other species (Chowdhury and Ward 1978). Grain number per panicle was not affected by temperature as high as 35/25°C, but yield was due to reduction in grain weight. Excessive high temperatures lead to head-blasting or abortion of grains (Jordan *et al.*, 1983).

Table 7.6 Regression coefficients of predictive equations: cv. CSHL

Phenophase	Eq.No. ¹	Regression parameters			r
		a	b	c	
GS1	2	29.5	-3.6*		0.51
	3	34.0	-3.6*	-0.07	0.55
GS2	2	49.6	-10.1**		0.71
	3	58.7	-6.8**	-0.23**	0.87
GS3	2	44.2	-5.8**		0.60
	3	43.9	-5.7**	-0.02	0.62
Days to anthesis	2	79.3	-13.7**		0.75
(GS1 + GS2)	3	92.9	-11.2**	-0.27**	0.86
Days to physiological maturity	2	120.5	-18.2**		0.70
(GS1 + GS2 + GS3)	3	133.2	-12.6**	-0.35**	0.83

1- a is the regression constant and b and c are regression coefficients; R= Correlation coefficient; probability= * at 5% level, ** at 1% level

Predictive equations:

2 $Y = a + b (19.6 - T)^{1/3}$ (with average temperature)

3 $Y = a + b (19.6 - T)^{1/3} + H$ (with average temperature and humidity)

T = average temperature, °C; H = average relative humidity, %

Leaf temperature

Plant leaf temperature is influenced by an energy exchange process between atmosphere and leaf tissue which is controlled by radiation, convection and transpiration. Leaf water deficits develop when there is increase in stomatal closure, causing decrease in transpiration and subsequently, a rise in leaf temperature. Transpiration reduces leaf temperature considerably (Gates, 1968; Van Boer and Ehrler, 1966). Miller *et al.* (1971) showed that leaf temperature and relative water content were highly correlated indicating that difference in leaf temperature is an indication of the plant water status. Carrison *et al.* (1972) reported that there was an increase in leaf air temperature differential whenever there was a decrease in relative water content. This is a direct consequence of stomatal closure and reduced rate of evaporative cooling. The leaf-air temperature differential is considered a stress-day factor.

Soil temperature

The soil derives its heat from 2 main sources: direct radiation from the sun and by conduction from the interior of the earth. The pattern of soil temperature

at different places depends on longitude, altitude, seasons and soil types. The soil surface temperature is coldest in the early morning and warmest in the early afternoon. The amplitude of the daily soil temperature wave decreases with depth in the soil. At midday heat is directed downward through the upper layer of the soil and the exit of heat from the middle of the layer begins after sunset but sometimes continues downward throughout the night (Rosenburg, 1974).

High soil-surface temperature affects the seedling emergence of sorghum (Wilson and Eastin, 1982; ICRISAT, 1982). The coleoptile bends downwards after reaching the high soil surface temperature regime. Cultivars showed significant variability in seedling emergence to soil surface temperature.

A study on 30 sorghum cultivars showed that 85% of them showed good emergence when the temperature reached a maximum of 38°C at seed depth, while only 36% emerged when temperature reached 48°C, a common occurrence in tropical soils (Andrews *et al.*, 1981).

The soil surface temperature has been found to influence seedling growth of sorghum (unpublished).

Sorghum grown at high altitudes is exposed to low temperature for germination. The minimum temperature for sorghum germination is about 10°C and slightly higher for emergence (Pinthus and Rosenblum, 1961). A down soil temperature of about 17-18°C at seed depth is reported to be satisfactory for emergence (Adams, 1965). Therefore, there is a necessity to select cultivars that can germinate at low temperature.

SOLAR RADIATION

Sun is the source of all the energy received on earth. It is the main source of energy which directs photosynthesis in plants and all other energy-consuming processes on earth. Solar radiation heats the soil, air, causes evaporation of water and this in turn affects the weather. Most of the solar energy falls in the wave length 300 to 3000 nm and is called short wave radiation. Sun emits long wave radiation ranging from 3,000 to 50,000 nm. All the solar energy emitted does not reach the earth's surface. Much of the ultraviolet radiations which are harmful to life are absorbed by water, ozone and carbon dioxide in the extraterrestrial atmosphere. Methane is an effective absorber of radiation. Water vapor has a major influence in retaining terrestrial radiation and in reducing its escape to space, thus, it helps in maintaining the energy balance on earth (Rosenburg, 1974). Some of the incoming solar radiation is reflected, absorbed and scattered by clouds and gases and causes sky radiation (Rosenburg, 1974; Yoshida, 1981). In the longrun, the amount of solar energy reaching the earth's surface to direct different energy-consuming processes is termed net radiation. In other words, net radiation is the sum of radiation received minus the short wave radiation reflected and long wave radiation emitted. This constitutes the radiation energy available on earth.

Green plants use a part of net solar radiation called photosynthetically active radiation (PAR) with wavelengths from 400 to 700 nm for photosynthesis. The ratio of PAR to total solar radiation is close to 500 nm in both tropical and temperate regions (Monteith, 1972).

The efficiency of photosynthesis of a crop depends partially on the interception of solar radiation by the crop canopy. Interception of solar light is maximum in the early morning and late afternoon when the sun's rays fall on the crop canopy at an angle. Interception is minimum when the sun is overhead. But there is a sharp increase in radiation intensity from 7:00 a.m. reaching the peak at 12:00 p.m. and there was gradual and sharp decline from 13:00 pm onwards in the month of January at ICRISAT, Patancheru, in India (17.5°N) when the sky was comparatively clear (Sivakumar and Virmani, 1980). There is a positive correlation between the interception and conversion of solar radiation into dry matter of the photosynthetic photoflux density (PPFD) by the sorghum crop (ICRISAT, 1981). Gross efficiency was calculated from the slope of the regression between cumulative intercepted PPFD, dry matter and the caloric value of the crop.

Research at Botswana (ICRISAT, 1982) has shown that net radiation measured above the sorghum crop was slightly higher for high plant population, perhaps because less radiation was reflected. Net radiation measured below the crop canopy showed considerable differences between high and low plant populations. The net radiation intercepted by the crop, calculated simply as the difference between measurements above and below the canopy was considerably larger for the higher populations. These trends were maintained throughout the growth, but were somewhat reduced towards the end of the season. These trends indicate that the pattern of net radiation distribution has important implications for water use by different populations densities. It seems probable that much more water moves *via* the crop pathway under high population while evaporation directly from the soil is greater under low population. Some of the energy below the canopy will be redistributed back to the crop layer by both radiant heat flux and sensible heat flux from the soil, so that differences in the volume of water moving *via* the crop pathways will not exactly match distribution of net radiation. Energy passing *via* the soil, i.e. soil heat flux, was maximum under low population. This energy raises soil temperature and is not used directly for evapotranspiration. Thus, in the absence of sensible heat from surrounding areas, net radiation above the canopy minus heat flux represents the total energy available from the crop and soil for evapotranspiration.

RELATIVE HUMIDITY

Humidity is expressed as a percentage of water vapor in the atmosphere at an existing temperature. Even with sufficient water supply to the crop, low humidity causes a daily water deficit. This may have a direct effect on the structure of leaf surface which in turn may influence the internal factors affecting transpiration (Slavik, 1973). The increase in transpiration from morning to mid-afternoon is the result of the increase in leaf air vapor pressure deficit.

O'Leary (1975) and Tromp (1977) concluded that although relative humidity played a significant role in plant growth and development, the literature on the effect of humidity is scanty. In recent years the effect of humidity on crop growth and yield has been reported in wheat (Hoffman and Jobs, 1978) and cotton (Bartsch, 1977), but there is little effect on phenology of the crop. In sorghum

Appathural (1957) observed that under high humidity (80%) the duration of the total lifecycle was shortened while under low humidity (50%), it tended to lengthen. Reddy (1979) and Reddy *et al.* (1984) observed that decrease in humidity caused delay in anthesis and the duration to physiological maturity. A probabilistic model has been derived by Reddy *et al.* (1984) in which the addition of humidity has improved the crop condition in GS2 (correlation coefficient increases from 0.71 to 0.87) than in GS1 and GS3. However, the effect of humidity is significant in the duration to anthesis and to physiological maturity (correlation coefficients increased from 0.75 to 0.86 and 0.70 to 0.83, respectively; Table 7.5).

WIND SPEED

Wind is defined as air in motion and its speed is measured with an anemometer and expressed in km/hr. An increase in wind speed may either increase or decrease transpiration or have no effect, depending on the temperature and vapor pressure deficit between leaf and air, concomitant changes in the resistance of leaf-boundary-layer and variation in internal leaf resistance (Monteith, 1965; Gates, 1968). If the saturation deficit of the air exceeds that at the surface of the leaf, the transpiration rate will increase with wind speed. But when the deficit is the same, transpiration will decrease with increase in wind speed if the deficit at the leaf surface is greater than in the air (Monteith, 1965).

DAYLENGTH

Daylength is the time interval between sunrise and sunset. The natural day length or photoperiod indicates the day length and, the duration of the twilight. Twilight is the time interval before sunrise or sunset, when the position of the sun is 6°C below horizon. House (1980) has made a concise review about the effect of daylength on floral initiation in sorghum.

As sorghum is generally a shortday plant sensitive to photoperiod, the vegetative bud does not flower until the daylength is short enough for the initiation of floral bud which is called the critical photoperiod. Tropical varieties will not flower in temperate zones, because the daylength during summer in the temperate zone never becomes short enough to reach the critical photoperiod stage. Therefore, before the advent of short days, the cultivars become very tall and plants are damaged by frost (House, 1980). Temperate varieties will flower when daylength is less than 12 hours. As plants are moved into the temperate zone, day length may exceed 13 hours. As this is a longer day than in the tropics exceeding the critical photoperiod of the tropical type, it remains vegetative. The temperate zone cultivar may need a critical photoperiod of 13.5 hours in which case a 13-hour day length is still shorter than the critical period at which the temperate cultivar will flower. Therefore, when days are shorter than the critical period, floral initiation occurs.

Daylength not only changes as one moves North or South from the equator, but also with the time of year. This change in daylength has a direct effect on floral initiation as does latitude. Therefore, cultivars having a critical photoperiod

of 12 hours or less cannot be used in the temperate zone unless and until the daylength is artificially reduced. A knowledge of the photoperiodic response of sorghum is of great value to breeders in planning their hybridization program.

RAINFALL AND SOIL WATER

Water is essential to maintain all the vital activities of the plant. Scarcity of water under rainfed agriculture retards the growth of the crop to a large extent. Therefore, in rainfed cultivars, water supply needs to be maintained either by rainfall or by irrigation. The plant absorbs water from the soil through roots, stems and finally to leaves, through which the plant loses water through its stomata.

Soil moisture

After application of water to the soil, some water known as gravitational water runs through due to gravity and drains below the root zone. The remaining water in the soil is known as capillary water and is held by capillary force. To extract capillary water, roots must exert a tension greater than that with which the water is held by soil particles. The moisture in the soil moves in response to water potential gradients, and also as a result of temperature gradient (Rosenburg, 1974). The root zone should have sufficient moisture for proper growth of the plant. Several forces operate in the aerial system, and the root region to maintain this dynamic flow of water from the root to leaves.

Movement of water in soil-plant systems

Perrier (1973) described the pathway of water transfer from the soil to the plant. Water moves in response to a potential gradient both in the soil and in the plant. The rate of water movement from the soil is largely controlled by the efficiency of the root system, soil temperature, concentration of soil solution and the free energy status of soil moisture. Changes in soil environment or aerial factors may alter water relations of the plants. For example, drying of soil or an increase in solar irradiation may increase the water deficit in the plant. Besides this, various plant responses counteract these changes in order to preserve water, reduce damage and maintain growth. The closure of stomata under dry conditions is a widely recognized response. Various other internal adjustment mechanisms also exist, for instance, accumulation of solutes in the cells may alter water relations.

Slatyer (1967) and Soman (1980) reviewed the role of solutes in water relations, discussing thermodynamic concepts in terms of soil-plant-water relations. They found that changes in solute content cause fluctuations in free energy of water in the cells. The solute component of the total potential is a function of the solute concentration and of any ionizations. Changes in the mineral supply may affect plant-water relations, but very little is known about this relationship. Mineral nutrients are necessary to maintain the osmotic pressure of the cell sap. Variations in water relations have been attributed to changes in the solute potential. Stout and Simpson (1978) found that changes in solute potential were associated with parallel changes in solute content.

The energy state of water expressed as water potential (Ψ) is the difference between the chemical potential, i.e., free energy of water in the system, and the

of pure water. Slatyer (1967) put forward the concept of free energy and water movement through the plant. The water in a tissue is held by 2 main forces, the solute potential (ψ_s) due to dissolved mineral potential and (ψ_p) due to the aqueous solution itself, which form the component potential of Ψ ($\psi_s + \psi_p$). A third force, the matric potential (ψ_m) due to the surface forces of the tissue also signifies the energy state of water. Therefore $\Psi = (\psi_s + \psi_p + \psi_m)$ where ψ_s and ψ_m are always negative, and ψ_p may be positive or zero).

The water potential system treats water in soil, plant and the atmosphere as parts of one continuous system. As water changes from the liquid to vapour at a given temperature, the chemical potential remains the same at equilibrium.

At field capacity of soil moisture, plant roots remain in equilibrium with soil water. However, under lower or near zero evaporative situations as happens during the night, losses of water are minimal, and leaf water status attains the level of equilibrium with soil water. To maintain the crop growth rate, it is essential to maintain an uninterrupted flow of water from the soil to the plant system, and any interruption in this flow of water has a direct effect on crop growth and development. The loss of water from the plant canopy is largely controlled by different microenvironments existing within leaves and around the canopy (Perrier, 1973).

Evapotranspiration

Penman (1948, 1956) defines potential evapotranspiration as the amount of water transpired per unit time by a short green crop of uniform height which completely covers the ground and soil, and which is never water deficient. When soil is maintained in a saturated state, evapotranspiration is primarily a function of energy responsible for transpiration and soil surface evaporation. Evapotranspiration is measured by different means in millimetres of water depth over the area considered.

Transpiration is the process by which plant releases water to the atmosphere through stomata in the leaves in response to the atmospheric demand. There are several plant characteristics that affect transpiration. Of these, location and distribution of stomata, reduction of transpiration surface (leaf rolling) and plant age are important.

Evaporation is the moisture lost in vapor from the soil surface. The amount of water available to the roots depends on the balance between rainfall and evaporation, and the relationship between soil moisture content, water potential and conductivity, effective rooting depth and water (Yoshida, 1981).

Evapotranspiration (ET) is affected by the following factors:

SOLAR ENERGY = ET increases with higher solar energies

TEMPERATURE = higher temperatures increase evaporation of water

WIND OR AIR MOVEMENT : a dry wind continuously sweeps away moisture vapor from a wet surface

RELATIVE HUMIDITY = ET is higher when relative humidity is lower and the capacity of air to retain water increases rapidly with temperature

PLANT CHARACTERISTICS = ET is influenced by leaf morphology, depth of rooting and duration of growth

SOIL WATER REGIME = ET is at maximum in saturated soils, but decreases with decrease in soil moisture content.

The knowledge of actual or potential evapotranspiration as given by Penman (1948) has wide utility, as well as other methods listed:

1. **HYDROLOGICAL OR WATER BALANCE APPROACH** - this includes methods such as catchment hydrology, soil moisture sampling and lysimetry.
2. **MICROMETEOROLOGICAL APPROACH** : This includes diverse methods such as aerodynamic or mass transport (perfile method: Eddy correlation method), energy balance (Bower ratio method) and combination of aerodynamic and energy balance method (Rosenburg, 1974).

Water balance

Water shortage causes a deficit of water balance in the soil and the plant, disturbing the proper course of all life processes in the plant, and results in failure of crop. The term 'soil-water balance' refers to the balance between moisture loss through evapotranspiration, runoff or drainage resulting in a change of soil moisture in the profile.

To adopt suitable crop management practices, it is necessary to quantify water available at the root zone of sorghum at different stages of crop growth. It is a difficult and timeconsuming process to quantify soil moisture at the root zone. Therefore, a suitable water balance model for predicting water balance will make the job easier for crop management specialists by means of accounting for surplus or deficit soil water. Water balance models provide useful means of evaluating land, and water management systems for better crop growth and crop production. Different water balance models have been developed by several researchers (Ritchie, 1972; Reddy, 1983). Soil water balance models can help solve several agricultural problems; development of agroclimatic models in establishing the length of growing period, adjusting crops to climates, assessment of fallow crop strategies, in the interpretation of considerable variability in crop yields between seasons and regions, and monitoring of supplementary irrigation (Reddy, 1984). In determining the soil water balance, evaporation is estimated. There are several approaches to estimate evapotranspiration. A realistic model takes into account differences among soil types, evaporative demand factors and crop factors such as type of crop cover, and the stage of crop growth.

Water use efficiency

Water shortage is the main factor limiting sorghum production in dryland areas. The growth and development of the crop in drylands depends on the efficiency with which the cultivars maintain growth with minimum water use. Jones *et al.* (1979) interpreted that the potential methods for increasing grain production in dryland agriculture are to modify land surface for better utilization of runoff water and minimizing soil water evaporation. Water use efficiency (WUE) can be expressed as the weight of dry matter produced per unit of water usage (Sullivan *et al.* 1980):

$$WUE = \frac{\text{Total biomass}}{\text{water use}} \quad \text{or} \quad \frac{\text{grain yield}}{\text{water use}}$$

They showed that WUE decreased as seasonal ET declined. Hybrid sorghum showed an increase in WUE under different irrigation treatments.

Response of sorghum to soil moisture deficit

Soil moisture deficit has a direct effect on crop growth. The first symptoms of

deficit of soil moisture in sorghum are wilting, rolling and twisting of plant leaves (Musick *et al.*, 1976). According to them, early in the crop season, grain sorghum has the remarkable ability to recover from the effects of deficient soil moisture, but irrigation after severe soil moisture deficit before heading of sorghum stimulates growth.

Leaf water potential

Soil moisture deficit has effects on leaf water content and stomatal conductance. Johnson *et al.* (1974) reported that the rates of net photosynthesis and transpiration of leaves and ears decreased linearly with decreasing leaf water potential.

According to Slatyer (1969) the level of plant water potential, and hence of internal water deficit, is influenced by 2 main factors: level of soil water potential and diurnal lag of absorption behind transpiration. Research on sorghum at Botswana showed that leaf water potentials of upper leaves were slightly higher in the narrower row spacings in both high and low populations throughout the growing season than in wider row spacings.

Stomatal conductance

Under decreasing tissue water, stomates close and the conductance of transpiration water decreases. Stomatal conductance was determined by measuring the rate of water flux (cm/sec) from the leaves with the help of the porometer. Sivakumar *et al.* (1981) showed that there was a gradual decrease in leaf water potential with age of sorghum crop and also with increase in moisture stress levels, because of the relative distance from the line source sprinkler system.

Stomatal conductance was influenced by the time of day and also by canopy depth. Under conditions of adequate water supply, stomates remained open from early in the morning until about 16:00 p.m. With decreasing irradiance, the stomatal conductance showed a rapid drop.

Using line source sprinkler, with a decrease in soil moisture with gradient inline source, there was a decrease in stomatal conductance and leaf water potential, and a rise in leaf temperature in sorghum (Sivakumar *et al.*, 1981).

Leaf-air temperature differential (stress degree day)

Drought induced stomatal closure caused by a decrease in leaf water potential, increases leaf temperature above the air temperature differential and was defined by Reddy *et al.* (1984) as stress degree day (SDD). The environmental stress imposed on leaves can be explained by considering the difference between leaf temperature and air temperature, the leaf-air temperature differential. This is strongly related to soil-water availability (Van Bavel and Ehler, 1966). High temperature causes leaf dessication and leaf firing in sorghum (ICRISAT, 1981).

There are several sophisticated techniques like porometer used to measure the water status of the plant but they are timeconsuming, and sometimes not reliable due to the extreme precautions required. These techniques can be used only on a small number of cultivars to avoid variation of plant water status.

Selection of genotypes for drought resistance

Plants have profound differential abilities to cope with drought. Crop cultivars are often exposed to depleting soil moisture conditions as a result of drought at different stages of plant development.

Drought at the seedling stage affects the establishment of seedlings and impairs

the development of roots, leaf expansion and initiation of reproductive meristems. Similarly, drought occurring at GS2 stage (panicle initiation to flowering) affects the normal development of the panicle thereby affecting the development of the florets and size of the vegetative shoot (source). Drought at the grainfilling stage affects the normal process of fertilization, seed setting and the size of grains. The effect of water stress on growth and development of sorghum was reported by Wilson and Whiteman (1965) and Bonnett (1979).

Effect of water stress on plant functions

Water stress is one of the wellknown causes of reduction in the growth rate of the plant, mainly due to either inhibition of cell division and/or enlargement (Kramer, 1969; Slatyer, 1973; Stocker, 1960). Water stress causes a decrease in pressure on the cell walls with the consequent separation of cellulose microfibrils. The emphasis is on inhibition of cell enlargement by water stress (Acevedo, *et al.*, 1971; Boyer, 1970). If water stress causes a decrease in leaf area, the number of stomata per unit area should increase provided stomatal differentiation is not affected. The rates of cell division and enlargement in stressed and unstressed leaves give an idea about the response of cultivars to water stress.

Bidinger (1978) reviewed the effect of water stress on plant development. Water for transpiration in plants comes mainly from the cellwalls lining the inner stomatal cavity; water loss in turn leads to a decrease in the chemical and water potential remaining in these cell walls. As water in the plant cells forms a continuous system throughout the plant, the negative potential is transmitted along with water in the xylem system from leaf to root. This creates a gradient between root and soil and causes water to move from the soil into the root. This potential gradient between leaf and soil is maintained by continued transpiration from the leaves.

Transpiration from leaves starts at sunrise and decreases in the evening. Atmospheric conditions favoring high rates of transpiration do not themselves induce large water deficits in the plant (Macklon and Weatherley, 1965). It is only when rapid water flux is coupled with the low water conductivity of the soil that high water stresses occur. The change in leaf ψ is transmitted to the absorbing surface (Weatherley 1970, Hsiao, *et al.* 1970) and absorption starts. But the entire water loss from leaves will not be compensated by absorption. Thus, a deficit for water develops in transpiring tissue. The magnitude of this deficit increases until the rate of absorption equals the rate of transpiration. This rhythm is repeated every 24 hours.

As diurnal rhythm of high and low ψ continues, the soil will no longer contain enough water to meet the daily evaporative demand and plant ψ declines progressively. Consequently, ψ in plants at dawn is also expected to become more negative. When this happens, the decreasing ψ plant at the root surface (root) fails to maintain the water flow to roots because of the drastic decline in the soil hydraulic conductivity with soil water content (Slatyer, 1967).

As ψ declines, the leaf turgor also declines for increasingly longer periods as the soil dries out. Finally, permanent wilting occurs when plant ψ at dawn equals to the solute potential at zero turgor (Slatyer, 1957 a,b).

The subcellular changes in sorghum leaves during water stress and subsequent rewatering are described by Giles *et al.* (1976). At -14 bars leaf water potential

stomata are closed, abscisic acid levels are elevated and the amounts of starch in the bundle sheath chloroplasts are much lower. The outer chloroplast membranes swell and the tonoplasts reorganize to form small vessels from the large central vacuole at a higher leaf water potential (ψ) of -37 bars. On rewatering, large amounts of starch reappear. The maintenance of tonoplast integrity is an important factor in the ability of plants to withstand drought. Reduction in cell division and cell expansion have a direct effect on leaf area index. As radiation interception is directly related to leaf area index, the photosynthetic efficiency of the crop is reduced.

Hsiao and Acevedo (1974) have summarized the mechanisms underlying the effect of water stress. Loss of tissue water may be due to the following physical and chemical changes: 1- the chemical potential or activity of cellular water is reduced, 2- turgor pressure decreases in cell, 3- small molecules and macromolecules become more concentrated in the plasmalemma and tonoplast, and membranes of organelles are altered as cell volume is reduced, 4- the effect on macromolecules might be through the removal of water of hydration or through modifications of the structure of adjacent water.

Hsiao (1973) stated that cell wall synthesis under water stress continued for a period even when there was no growth due to lack of turgor in the stressed plants. Cell division appeared to be as sensitive as cell expansion to prolonged water stress (Gardner and Nieman, 1964), while in other cases cell division appeared to be less sensitive. The sensitivity of mitosis to prolonged mild stress may be an indirect result of reduced cell expansion. Under severe water stress, turgor pressure may come down to zero and under such a situation, plants can maintain some growth through osmoregulation, a mechanism of solutes build up in the cells so that turgor pressure can be developed inspite of low water potential. Hsiao and Acevedo (1974) suggested that one of the earliest tests for a breeder in selecting drought resistant plants (or even plants with higher wateruse efficiency) would be to determine the ability of the plant to maintain expansive growth at reduced water potential.

Effect of water stress on leaf growth

Growth can be defined as an increase in dry weight or leaf area. The rate of growth is, therefore, the change in weight or area per unit time. These differences result from physiological and biochemical processes. Environmental factors such as water stress affect at least some of the mechanisms causing changes in the rates of the processes (Soman, 1980).

Leaf growth of many crops is inhibited by water stress; such is the case with wheat (Ford and Thorne, 1974; Connor, 1975; Sands and Correl, 1976; Quarrie and Jones, 1977; Rawson *et al.*, 1977); Maize (Lawton, 1969; Boyer, 1970; Hsiao, *et al.*, 1970; Kleinendorst, 1975); sorghum (McCree and Davies, 1974; Kaigama *et al.*, 1977; Stout *et al.*, 1978); and barley (Nicholas and May, 1963; Hussain and Aspinall, 1970; Biscoe *et al.*, 1975).

It is generally believed that water stress affects leaf growth but observations vary and opinions differ as to what stress affects and how stress operates. Reduction in leaf area may result from small leaf size and/or decreased leaf number. Leaf size is the outcome of the leaf expansion rate and the duration of growth;

leaf number depends upon leaf initiation and senescence. Water stress has been found to affect all these processes. Leaf expansion depends upon cell division and cell enlargement. Attempts have been made to relate variation in leaf area due to water stress to either cell division or enlargement. Earlier cessation in cell division along with smaller cells has been observed in sorghum (McCree and Davies, 1974), wheat (Quarrie and Jones, 1977), and maize (Kleinendorst, 1975).

Effect of water stress on inflorescence development

Flowering in cereals is thought to be sensitive to water stress. The rate of appearance of floral primordia appears to be reduced by mild water stress.

The effect of water stress on inflorescence development in sorghum appears to be somewhat different from those on other cereals (Wilson and Whiteman, 1965). When severe stress was applied for about a week at the time of inflorescence growth, it ceased. Yet upon rewatering, panicle development apparently proceeded unaffected, and the number of grains was not significantly different from control plants.

Mechanisms of drought resistance

Different mechanisms exist in crop plants to resist soil moisture stress (Lerman, 1972). Jordan and Monk (1980) have reviewed sorghum literature related to various mechanisms for avoidance or tolerance of drought and indicated that avoidance mechanisms provided the greatest opportunities for yield maintenance. Reactions and resistance of grain sorghum to heat and drought have been discussed by Jordan and Sullivan (1982):

Drought escape

Escape mechanisms to resist drought operate in sorghum in 3 ways - early maturity, developmental plasticity, and remobilization of stem reserves (stored before anthesis) to grain.

Early maturity

In much of the Indian peninsula, early maturing hybrids and varieties of 100-110 days duration are known to escape the effect of a late drought and have replaced the traditional sorghum types with a duration of 130-180 days. This has resulted in a remarkable increase in sorghum production in spite of intermittent drought on early maturing genotypes in proportion to their lower leaf area index and lower root density. Blum (1970b) has demonstrated the yield advantage associated with early maturity for dryland sorghum grown in the mediterranean climate. Early maturity has greater potential in cultivars where growth is achieved on stored moisture.

Drought avoidance

For the same level of soil moisture stress, some sorghum genotypes consistently maintain higher leaf water potentials (Blum, 1974 a,b and 1975a). This phenomenon is independent of leaf rolling which serves to reduce the effective leaf area per plant (Begg and Turner, 1976). Drought avoidance is achieved by increased root growth or by maturity before the onset of drought. Genotypic differences in sorghum roots have been found to exist (Blum *et al.*, 1977 a,b; Jordan *et al.*, 1979). Screening methods using nutrient culture (Jordan *et al.* 1979) or brick chambers have been found satisfactory for seedling drought studies.

Drought tolerance

The response and tolerance of plant tissue to reduction in leaf water potential may involve a number of physiological and metabolic processes. Maintenance of growth and interpretation of results are difficult to assess due to complex interactions in size among the organs (Blum, 1973; Begg and Turner, 1976).

Heat and desiccation tolerance and ability to recover from stress

The usefulness and practicality of testing for heat and desiccation tolerance were reviewed by different authors (Arnon, 1975; Sullivan and Ross, 1979).

Osmotic adjustment

Diurnal and seasonal osmotic adjustment in response to water stress has been reported in sorghum by Jones and Turner (1978) and genotypic differences for this trait were studied by Stout *et al.* (1978). Under conditions of high atmospheric demands for water, a decrease in osmotic potential was shown to contribute to leaf expansion in sorghum (Acevedo *et al.*, 1971). Thus, we find that different mechanisms exist in sorghum to withstand drought, and genotypes show a wide range of variability to drought response.

Jordan and Sullivan (1982) stated that maturity, root system diversity, epicuticular wax loads, osmoregulation, heat and desiccation tolerance play an important role in determining the avoidance mechanism in sorghum. Genetic variability has been demonstrated by several authors (Jordan and Monk, 1980). High root to shoot ratios of young plants have been correlated with superior drought resistance (Nour and Weibel, 1978; Bhan *et al.*, 1973). Increased rooting depth will increase total water availability for the plant (Jordan and Miller, 1980). The aerial surfaces of most sorghum cultivars are covered with a thick, amorphous layer of epicuticular wax. In addition, normal or bloom types show the presence of wax filaments on peduncle, leaf sheath and basal portions of the abaxial leaf surface giving a a fluffy, white appearance. Epicuticular wax is said to enhance drought resistance. The presence of the waxy bloom is controlled by a single, dominant gene. Several bloomless and sparse bloom variants are reported (Ayyangar and Ponnaiya, 1942; Ayyangar *et al.*, 1937). Consistent yield advantage of waxy bloom is observed in water deficient environments (Ross, 1972; Webster, 1977; Webster and Schmalzel, 1979). Chatterton *et al.* (1975) reported that transpiration is lower in waxy bloom isolines. Genotype response across environments over the years was variable in some cultivars that maintained high epicuticular wax loads (Ebercon *et al.*, 1977; Powell *et al.*, 1977; Jordan and Miller, 1980).

The role of high epicuticular wax loads is considered to be important to leaf survival rather than to maintenance of high productivity since its principal function is to retard water loss via the cuticular pathway (Jordan and Miller, 1980). Osmoregulation is defined as osmotic adjustment by cells through synthesis and accumulation of solutes in response to water deficits. The solutes are a complex mixture of organic acids, amino acids and sugars. This mechanism of osmoregulation serves as a means to maintain turgor as tissue water potentials fall and growth is retarded (Hsiao, 1973).

Two cultivars, RS 610 and Shalu, differ in drought resistance, but did not show differences in their osmoregulatory capacity (Jones and Turner, 1978; Turner and Jones, 1980). Blum *et al.* (1977 a,b) demonstrated cultivar differences in the

capacity to accumulate proline in response to water stress. Blum (1979 a,b) suggested that proline may be an important energy source during recovery from water stress. Hensell *et al.* (1975) reported cultivar differences in stomatal sensitivity to water deficit but large-scale screening was not attempted. Ackerson *et al.* (1980) reported osmotic adjustment of lines and hybrids subjected to drought in the field.

Sullivan (1972) described a simple method to evaluate heat and desiccation tolerance based on loss of membrane integrity of leaf tissue following stress under controlled conditions. Heat tolerance has been positively correlated with yield when crops are exposed to heat and drought stress (Sullivan and Ross, 1979). Genotypic variability exists in sorghum for both heat and desiccation tolerance (Sullivan 1972; Blum and Ebercon, 1976; Sullivan *et al.*, 1977; Sullivan and Ross, 1979), but parallel ranking between the 2 tests were not obtained (Sullivan and Ross, 1979).

SCREENING

Several approaches for drought resistance screening have been advocated (Seetharama *et al.*, 1984). These may be either direct or indirect selection for resistance and explain either selection for absolute performance of crops under actual stress conditions or selection for a small reduction in growth and components under stress compared to unstressed plants. Indirect selection implies screening for morphological or physiological characteristics which appear to be related to drought resistance (Maiti, 1981). Evans (1980) stated that empirical selection is likely to remain the most effective procedure. Direct selection from field screening often fails due to sudden and unexpected rains. Field screening could be done at sites or in seasons where there is little or no rainfall or where moisture supply can be controlled. Warmer parts of the dry season are preferred as the temperature and radiation levels tend to be high and vapor pressure low, all favouring high transpiration rates when soil moisture supplies are inadequate to meet the demand.

Selection for desiccation and heat tolerance was adopted by Sullivan and Ross (1979) and for stomatal sensitivity to stress by Hensell *et al.* (1975). Use of these techniques to evaluate germplasm is difficult to achieve. Therefore, to evaluate a large number of germplasms and breeder lines, priority should be given to field screening. The selected lines can then be subjected to various tests for investigating the underlying drought resistance mechanisms.

Breeding strategies

Strategies for breeding for drought resistance have been discussed by various authors (Blum, 1979 a,b; Hurd, 1976; Sharma and Saxena, 1979; Townley-Smith and Hurd, 1979). According to Nederski and Jeffers (1973), a superior yielding variety under optimum conditions will also give good yields under suboptimal conditions. Stability of yields over various environments would lead to accumulation of stable yield genes which perform under stress situations (Blum, 1973).

Blum (1973) outlined some approaches for improving drought resistance in sorghum: 1- the improvement of yield performance under conditions of drought stress should be associated with an improvement of yield at potential levels. 2- selection of superior varieties under drought conditions may be less adaptable to the relevant environments even as breeders attempt to manipulate yield genes.

Varieties developed in such a program are grouped for high genotypes X environment interactions. At subpotential levels, heritabilities for yield and yield components are relatively low and selection for yields is not efficient (Johnson *et al.*, 1974); 3- a combined research approach supported by background research in plant breeding and plant physiology may provide genetic improvement for drought resistance.

At ICRISAT, many simple techniques have been developed to screen sorghum germplasms and breeder lines for drought resistance at seedling stage under semi-controlled conditions in brick flats, PVC cylinders and also in the fields. Significant genotypic differences in response to drought at seedling stage have been found both in the germplasms and breeder's elite lines, as measured by scores for wilting, recovery and survival after the release of stress. Many of the lines resistant to drought at the seedling stage have been observed to have light green leaves with a glossy surface, while the susceptible lines, generally have dark green leaves. About 21,000 germplasm accessions have been screened for the "glossy" trait and about 520 glossy lines have been identified. These lines are being tested for drought resistance.

Field screening at ICRISAT, attempts have been made by physiologists to evolve simple, direct empirical drought screening methods to evaluate germplasms and breeder's lines. The experiments were conducted under soil moisture stress in the post-rainy and summer seasons. Initially this was confined to 1- drought during the panicle development stage, and 2- conditions of receding soil moisture in vertisols. The former represents the midseason drought pattern of the rainy season in many parts of SAT and the later shows similarity with the crop grown under receding soil moisture conditions in Israel as well as in parts of West Africa.

The line-source-sprinkler irrigation (LS) proposed by Hanks *et al.* (1976) is useful to maintain a stress gradient with minimum land and cost. A single row of overhead sprinklers produces a gradient of water application pattern. A series of test rows of different genotypes at right angles to the line source can be planted. Each row is thus being exposed to a uniform gradient of water from zero to any desired maximum. Genotypic differences in response to declining water supply can be detected when yield is plotted against water applied through LS. The intercepts and slopes of regression equations indicate yield potential and plant susceptibility to gradual decline in water supply, respectively. Genotypes with higher intercepts and lower degree of slopes are selected. This technique is being used at ICRISAT; experiments were conducted to evaluate 1- relationships between soil water and crop growth, 2- development and yield, and 3- usefulness of the technique to screen sorghum genotypes for drought resistance.

GENERAL COMMENTS

An account of crop environment clearly shows that growth and development of a crop is largely dependent on interaction of microclimates with crop canopy. A knowledge of these microclimates is an essential prerequisite to adopting suitable crop management practices. This chapter emphasizes that the sun is the

source of all energy, guides the energy-driven processes on earth and governs the climates. We have discussed how different environmental components affect growth, development and yield of sorghum, especially in the adverse climatic conditions of SAT. Several techniques have been formulated to evaluate cultivated germplasms and their responses to plant environments. There is a need to select cultivars adaptable to diverse environments. Simulation modeling could help predict the growth and development of crops under diverse climates and different environments. Simulation models can estimate the yield from a region with widely variable rainfall and a range of soil and crop management practices. This approach could be utilized to develop plant ideotype and predict crop growth and growth stages. The crop growing conditions of semiarid regions cannot be substantially improved although some improvement could be made by adopting good management practices. Plant productivity can also be improved by developing plants capable of withstanding unfavorable environments. More research effort is needed to improve crop productivity in unfavorable environments.



MINERAL NUTRITION OF SORGHUM¹

INTRODUCTION

All living organisms require mineral elements to sustain life and to grow and develop, and each organism is different in its requirement for specific mineral elements. Sorghum is a cereal and cereal crops have mineral element requirements that are different from noncereal crops. This is specifically true for nitrogen (N), since cereals do not now have the capacity to fix their own N from the atmosphere. Even within the cereal crops, sorghum is different from the other species of this group. Compared to maize, sorghum may be considered to require lower amounts of mineral elements, because of different growth rates and amounts of dry matter produced.

Without adequate supply and balance of mineral elements, sorghum will not grow well and produce adequate or desired end-products (grain and/ or fodder). Environmental conditions, soil type, capital assets, cultural practices and other factors dictate the amount of mineral elements used for the production of sorghum crop. Conditions are unique to nearly every place where sorghum is grown. Therefore, general statements about mineral element requirements for the production of a particular sorghum crop are difficult to make. Many factors must be considered.

The objectives of this chapter are to discuss each mineral element separately and to give concepts about some of the aspects unique to each element relative to mineral nutrition of sorghum, and to plants in general, with the hope that this approach will help to understand specific peculiarities associated with the mineral element requirements of sorghum and to provide information whereby better decisions can be made about mineral element problems, applications and use.

MINERAL ELEMENT REQUIREMENTS

Many factors are involved in determining mineral element requirements for the production of sorghum. Some factors that must be considered are: 1- the amount of available and residual mineral elements in soils, 2- chemical and physical

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properties of soils, 3- environmental conditions of the soil and locality, and 4- yield and end-product desired.

Three of these factors can be controlled to some extent by the addition of fertilizers and amendments according to needs of plants and soils. Except for moisture (irrigation), pest control, and cultural practices, little can be done about the control of some of the other environments conditions. The amount of product desired can be programmed, and the amount of seed sown can be controlled but ultimate yields remain the effect of all factors combined.

In general terms, the amount of mineral element removed by a sorghum crop producing approximately 8,000 kg/ha grain are (in kg/ha): 250 Nitrogen (N), 160 Potassium (K), 45 Magnesium (Mg), 40 Phosphorus (P), 40 Sulfur (S).

The amount of calcium (Ca) and the micronutrients (manganese (Mn), iron (Fe), boron (B), copper (Cu), and Zinc (Zn) removed are considerably less. Some mineral elements will be recycled if the fodder is left or added to soils, if it is removed from the soil, higher amounts of these elements will also be required.

As sorghum plants grow, mineral elements are taken into plants at different rates and amounts. Young plants usually absorb relatively high amounts of the mineral elements, and with age some elements are transferred from one plant part to another. Mineral element concentrations in various plant parts vary with plant age (Table 8.1), as well as the total amounts of each element absorbed as plant age (Table 8.2), and the distribution of mineral elements in various parts at maturity are given as a reference for changes that may occur in sorghum plants grown in the field (under relatively optimum conditions). As each element is discussed, reference to these tables will be helpful to understand its uptake, accumulation and distribution in sorghum plants.

Nitrogen

Of all the mineral elements required for sorghum growth, N is one of the most abundant elements in the plant. It is usually added to soils to meet sorghum plant needs. Nitrogen for plant growth must be either applied, provided through atmospheric fixation, or obtained from residual sources in the soil. For maximum plant yields, N is usually applied with each sorghum crop and sometimes added more than once during the plant growth cycle or season. Nitrogen is usually the most expensive mineral element that is required for sorghum production.

The lithosphere contains relatively high N, but the soil portion of the lithosphere is very small compared to the whole. Most lithospheric N is inaccessible or unavailable for plant use. The portion of N potentially available for plant use in soils is found in various forms and is constantly changing. Even though atmospheric N may be fixed by microorganisms or plant-microorganism association, this source of N is not readily available to sorghum until the N is converted from organic to inorganic forms. The interconversions of the various forms of N [organic N, ammonium (NH_4^+), nitrate (NO_3^-), and gaseous N] and the use or loss of NH_4^+ and NO_3^- are continually changing. Because of the dynamic changes that occur in N in soils, the amount of available N can change extensively in a relatively short period of time. Nitrate levels in soils may be as high as 20 to 30 mM after a fertilization, but normally range from 2 to 20 mM in soil solutions. Only about 50% of the N applied to soils is taken up and used by plants. The remainder is

Table 8.1 Mineral element concentrations in aboveground sorghum plant parts with age.

	Vegetative			Bloom/early grain fill - 12 leaf	
	PLANT	LEAVES	STALK	HEAD	PLANT
N *	20.4	28.6	11.0	23.3	17.9
P *	3.17	3.09	2.40	4.21	2.76
K *	40.2	14.4	20.8	8.9	19.8
Ca *	28.6	41.1	23.2	5.5	28.6
Mg *	2.18	2.54	2.87	3.45	2.82
S *	1.40	1.36	0.90	2.00	1.14
Si *	21.8	23.8	17.3	1.0	18.8
Mn **	41.2	39.8	40.4	28.6	39.6
Fe **	274	196	62	41	108
Cu **	7.4	8.4	7.9	10.7	8.4
Zn **	21.3	20.1	27.2	38.8	25.6
DMY ***	58	80	131	13	224
Maturity					
	LEAVES	STALK	GRAIN	WHOLE PLANT	
N *	19.6	6.0	13.7	13.0	
P *	1.80	1.12	2.96	2.29	
K *	10.0	24.6	5.7	11.1	
Ca *	58.4	25.3	1.3	18.4	
Mg *	2.30	2.56	2.16	2.28	
S *	1.20	0.87	1.03	1.03	
Si *	41.2	26.6	0.3	14.7	
Mn **	72.9	24.9	10.8	26.5	
Fe **	393	67	33	112	
Cu **	7.9	7.5	4.2	5.7	
Zn **	22.8	21.2	14.0	17.5	
DMY ***	88	106	249	443	

* mg/g dry weight; ** $\mu\text{g/g}$ dry weight; DMY dry matter yield (g/plant)

left for microorganism use, leaching, or other N reactions and processes that occur in soils.

Nitrogen deficiencies occur on essentially all soils, whether they be alkaline, neutral, or acid. The various reactions for and changes in N depend on many factors, but the presence and sustenance of microorganisms is important. Nitrogen in soils with adequate or high moisture will change more extensively than in drier soils.

Both NH_4^+ and NO_3^- (inorganic N) can be absorbed by plants, but NO_3^- is

Table 8.2 Proportion of mineral elements in sorghum plants with age.

	Stage of plant growth (contents as % of total at maturity)		
	Vegetative 12 leaf	Bloom/early grain fill	Maturity
Dry Matter	13	50	100
N	20	70	100
P	18	61	100
K	47	90	100
Ca	20	78	100
Mg	12	62	100
S	18	56	100
Si	19	64	100
Mn	20	76	100
Fe	32	49	100
Cu	17	73	100
Zn	16	74	100

usually found in higher proportions than NH_4^+ under most soil conditions. Ammonium at excessive concentrations can be toxic to plants. Most inorganic N is rapidly converted to an organic form once inside plant tissue, but NO_3^- is commonly noted in plant tissues.

Nitrogen concentrations in normal sorghum leaves range from about 15-30 mg/g (dry wt). Nitrogen is a constituent of numerous organic compounds in plants, specially amino acids (the building materials for proteins), nucleic acids, and other cellular compounds. Since enzymes (proteins) catalyze nearly every metabolic reaction in plants, N is indispensable to plant growth and development. Young plants accumulate relatively high concentrations of N, but N decreases in the various plant parts with age. Nitrogen is readily remobilized. It is transferred from one plant part to another, and accumulates extensively in kernels. Most of the plant N is absorbed during the vegetative and by early grainfilling growth stages.

Plants deficient in N usually are stunted, spindly and pale yellow in color. Symptoms appear first on older (lower) leaves and spread to the younger (upper) leaves. A uniform pale or deep yellow color develops near the tips and margins and progresses toward the base and midrib of the leaf. Necrotic spots normally develop when severe deficiency symptoms appear. Severe N deficient leaves turn brown, die and fall down (pendent) on the plant. Heads of N deficient plants are small, yields are reduced, and seed numbers are reduced. The vegetative stage of plants is shortened and plants usually mature earlier. Shoot/root ratios normally increase with N deficiency.

Supraoptimal N may promote lush, green foliage and delay maturity. Ammonium is normally toxic at lower levels of N than NO_3^- . Excess NO_3^- causes leaf margins to appear water-soaked, turn dark green, and be somewhat leathery in texture before dying and turning dark brown or black.

Phosphorus

Although abundant amounts of P are usually absorbed and accumulated in sorghum, the actual amounts of P needed in metabolic reactions and structural components of cells are relatively small. Considerable amounts of P are normally added to soils on a consistent basis, usually annually or with each crop. Some estimates show that only about 10 % of the P added to soils is absorbed by plants. Therefore, extensive amounts of P become unavailable in the soil by absorption or fixation by various soil fractions and particles. Soil P concentrations of about 1.1 mM (near 3 $\mu\text{g/g}$) are considered adequate for plants. For plants fed adequate P, about 60 to 80% of the P inside plant tissues is considered to be in the organic form. Thus, considerable amounts of P inside plants are not performing essential functions at all times. The turnover rate of P in metabolic reactions is rapid, because P has a primary function in energy transfer reactions of the various metabolic pathways. P is involved with nearly every metabolic process in the plant, and P deficiency can directly or indirectly affect nearly every plant growth process, including energy transfer reactions.

Phosphorus interacts with many elements, so the availability and function of other elements is affected by P. P exists in 3 anionic forms (PO_4^{3-} , HPO_4^{2-} , and H_2PO_4^-). Young plants usually have relatively high P concentrations which decrease with age. Normal concentrations range from 2 to 4 mg/g. Phosphorus accumulates extensively in the kernels (as phytin). Phosphorus is readily remobilized from older to younger tissues and from vegetative tissue to the grain. As P is readily mobile, deficiency symptoms appear first on the lower (older) leaves and progress upward toward the upper leaves. Most of the P absorbed by plants is taken up by the grain fill. As the plant matures, considerable amounts of P move from the vegetative parts to the grain. At maturity, over 70% of the above ground plant P is found in the kernels.

Phosphorus supply and availability for plants grown in low or P deficient soils may be altered greatly by mycorrhizae species associated with plant roots. These mycorrhizal associations with sorghum (and other plants) are not abnormal or exotic, because the greater part of the vegetation worldwide is infected with them. The two major classes of mycorrhizae fungi identified are: 1- ectohopich which forms external mycelia sheaths around roots and between cortical cells and are associated exclusively with 3 species; 2- vesicular arbuscular whose mycelia grow both internally and externally to root cells, extend extensively from roots into the surrounding soil and are found with roots of nearly all plant species. Four major genera of vesicular arbuscular mycorrhizae (VAM) fungi have so far been found to be associated with sorghum: *Glomus*, *Gigaspora*, *Acaulospora* and *Scherocystis*. In pot culture experiments, certain VAM fungi increased plant dry matter yield by as much as 220 % over plants grown without mycorrhizae. The VAM species showed differences in effectiveness for plant dry matter increases. Phosphorus concentrations increased by as much as 3-fold in sorghum grown with VAM fungi. VAM fungi have been known to enhance not only P absorption, but also K, S, Zn, Cu and Si absorption in plants. The magnitude of mycorrhizae response has usually been much greater for P than for the other elements. Even though VAM fungi contribute only about 10% to the total dry weight of roots, they have the

potential of absorbing P at rates many times that of uninfected roots. Increased P uptake by plants associated with VAM cannot be accounted for by P diffusion in soils, because P diffusion in soils is so low. Mycorrhizae increase the effective soil volume from which roots can effectively absorb P and other mineral nutrients. The VAM fungi themselves also have the potential to make P more available for plant uptake.

Population densities of mycorrhizae are associated with levels of P in the soil. If soils are low in P, mycorrhizae densities are higher than in soils with higher levels of P. Supraoptimal levels of P appear to be toxic to mycorrhizae. Increases in productivity of crops like sorghum grown in soils with low or deficient levels of P may be greatly enhanced if adequate mycorrhizae infection with highly efficient strains are obtained. Even though genotypes differ in their ability to tolerate low P, tolerance to low P may be associated with root mycorrhizae.

Phosphorus deficiency occurs frequently when plants are grown on acid and tropical soils. These soils (usually oxisols and oxisols) generally have high fixation capacities for P because of high Al and Fe oxide concentrations. Phosphorus does not readily move in soils because of its high reactivity with soil particles. For the most part, plant roots must grow to where P is located to adequately supply plant needs. Because of the low P mobility in soils, considerably more P is added to soils than is absorbed by plants.

Phosphorus deficiency in plants is relatively common during cool weather. In the temperate zones, seeds are planted and seedlings are small during much of the cool weather. As a result, small plants with their relatively small root systems, cool root environments, and fairly high P demand often show P deficiency symptoms during the early plant growth stages. Phosphorus deficiency tends to decrease tillering and may be the result of decreased phytohormones needed to assure the formation and development of new tillers. Shoot growth appears to be affected more by P deficiency than root growth, thus shoot/root ratios generally decrease as plants become P deficient. Grain development and filling are inhibited by P deficiency, so kernel quality is usually poor.

Deficiency of P is characterized by stunted, spindly, dark green leaves which have overtones of dark red coloration. Older leaves show the red pigmentation first, and this pigmentation progresses upward toward the younger leaves. Leaf tips and margins show the redness first which progresses toward the base and midrib. A characteristic symptom of P deficiency on leaf sheaths is also the upward progression of red coloration. At times the dark red coloration of P deficiency will occur in streaks in the interveinal tissue leaving green veins. As the deficiency becomes more severe, the red pigmentation will become uniformly distributed over the leaf. If the deficiency continues sufficiently long, leaves turn brown and die. In young plants, leaves often appear to be more erect and sometimes "leathery". Roots often turn dark brown, purple or black.

Excess P can depress plant growth and interact with other elements (especially Fe, Cu, and Zn) to cause deficiencies of other elements. Reduction of root growth by excess P has been noted. Supraoptimal P has also been shown to cause a unique "red-speckling" on the tips and margins of older leaves of many sorghum genotypes. This "red-speckling" decreases progressively from older to younger

leaves. This disorder appears at the tips and margins and progresses toward the base and midrib of leaves. The amount of P in the soil or growth medium to induce this disorder is relatively low (often less than 1 $\mu\text{g/g}$). This disorder is not induced in older plants as readily as in younger plants, but if sufficient P is added, it can be induced on older leaves as well.

Potassium

Potassium is one of the most abundant mineral elements in sorghum plants. Depending on plant age, plant part and conditions, other mineral elements to approximate K in plant composition are N, Ca and Si. Because K accumulates in sorghum plants at relatively high concentrations, considerable amounts of K must be added to soils or soils must be adequately supplied with available K. Neutral to alkaline pH soils normally contain high amounts of residual K. Potassium normally has to be added to acid soils because of its depletion by leaching from the relatively high amounts of rainfall.

Even though some soils contain considerable amounts of K, most of it is associated with nonexchangeable fractions. Exchangeable K levels in soils vary, but are usually at about 2 to 5 $\mu\text{g/g}$ soil and represent about 1 to 4% of the total soil K. Factors such as source of parent material, type of clay, amount of fixation and organic matter affect the amount of soluble or exchangeable K available for immediate plant uptake and use. The nonexchangeable fractions of soil K are structural K (soil minerals) and absorbed K (on clay and organic matter colloids). Even though the amount of exchangeable (free) K may be low, many soils have the potential to make considerable amounts of K available. However, the rate of availability may be limiting and insufficient for immediate plant needs, and additional soluble K may be required for optimum growth. Of the K applied to soils, only about 30 to 50% is absorbed by plants.

Potassium is absorbed by plants readily as K^+ and this is the active form inside plants. Concentrations of K in plants are usually around 20 to 50 mg/g (dry weight). Inside the plant, K does not form stable complexes, is not bound tightly and is not an integral part of organic molecules. Potassium functions primarily in osmoregulatory processes like cell turgor, stomate opening and closing, and protein configuration and conformation. Potassium functions as a catalyst of numerous enzymes; over 70 enzymes have been identified that require K for maximum activity. In the metabolic processes or enzymes requiring K, relatively high concentrations are reported for optimum activity. *In vitro* experiments often report 40 to 80 mM K for maximum activity of enzymes and 100 to 200 mM K are not uncommon in cellular cytoplasm and vacuoles. Potassium has been associated with cellular electronegativity. That is, if excess anions appear in the cells from NO_3^- absorption and organic acid synthesis, K^+ is the usual counter-ion associated with these compounds. Potassium has also been associated with the circulation of organic and aminoacids in the transport systems of plants. Potassium is highly remobilized and readily moves during plant development from older to younger tissues if the need arises.

Young sorghum plants accumulate high K in the leaves which decreases with age. Although kernels contain considerable K, most of the plant K in older plants remains in the stalks. Potassium deficient plants lose stalk strength and are prone

to lodging. Most of the plant K is absorbed by the grain fill stage of plant development. Adequate K in plants has been associated with higher tolerance to drought, higher resistance to frost and salt damage, and higher resistance to fungal attacks.

Potassium deficiency in plants may not result in visible symptoms before reductions in growth appear. Symptoms of K deficiency appear first on older leaves and then spread to the young leaves. Irregular necrotic patterns intermingled with red pigmentation characterize visual K deficiency symptoms. Sometimes streaked patterns occur on the interveinal tissue, but the symptoms are fairly uniform over the leaf. Symptoms begin at the tips and margins and move toward the base and midrib of the leaves. The unaffected portions of leaves remain fairly green. It is often difficult to distinguish a K deficiency from "red-speckling" caused by excess P. Potassium deficient plants do not normally show the spindly growth observed for N and P deficiencies. Shoot/root ratios remain fairly constant with K deficiency and grain yields are frequently reduced.

Excess K disorders seldom occur unless plants are grown under abnormal conditions like saline soils. Excess K causes leaves to become uniformly pale, become water soaked, die and turn brown. The symptoms progress from the tips toward the base of leaves and are usually more severe in the older in the younger leaves.

Calcium

The amount of Ca needed by sorghum is fairly high during vegetative growth but not during reproductive growth. Leaf concentrations of Ca vary widely and concentrations of 50 to 70 mg/g dry matter are not uncommon. Thus, a readily available source of Ca in soils is needed for plants. Many soils normally contain adequate or high Ca (alkaline and calcareous), but acid soils are often low in soluble Ca. Because of this, Ca deficiencies seldom occur in plants grown on alkaline or neutral pH soils, but occur frequently when grown on acid soils. Soluble Al and Mn in acid soils also interact with Ca to enhance Ca deficiencies in plants. Acid soil problems are usually corrected by lime amendments, which is a source of Ca to overcome Ca interactions with Al and Mn.

Calcium is taken into plants as a cation (Ca^{2+}) and remains in this form for all functions. Calcium can be complexed fairly readily, usually with organic acids. Calcium functions in plants are associated with membranes (conformation, integrity, leakiness, secretion, ion pumps), cells walls, a few enzyme reactions, phytohormone regulatory reactions, osmoregulation, pollen tube growth, cell division and mitosis, and gravi-, photo- and thigmo-tropic processes. Leaves normally accumulate late relatively high Ca. This is not remobilized when Ca deficiencies appear in other tissues. Very little Ca accumulates in kernels. Most plant Ca is absorbed during early grain fill.

Calcium deficient plants become stunted because of death of newly emerging and developing tissues. Ca deficiency occurs first in the meristematic tissues. Young leaf tips often stick together (ladder-like effect), form sword-like projections, have serrated (torn and warped) leaf edges, and often show lightly bleached leaf margins. Severe Ca deficient leaves are brittle and form brown, sticky vesicles at or near the margins. The leaves frequently coalesce and turn brown. As Ca is mobile primarily in the xylem (upward translocation stream), older leaves usually

contain adequate or high concentrations of Ca and young leaves and even sections of leaves may be low in Ca. When plants overcome Ca deficiencies after Ca deficiencies, leaves often show aborted, twisted symptoms with leaf tips sticking together as new plant leaves begin to regrow. If Ca deficiency persists, heads will not form because primordial and meristematic tissues are destroyed. Shoot/root ratios usually decrease with Ca deficiency, because shoot growth is affected extensively.

Calcium deficiencies often occur in sorghum plants grown in greenhouses and growth chambers. These Ca deficiencies appear to be associated with reduced transpiration and restricted root growth in pots. High light intensity, certain types of drought and high temperatures tend to enhance Ca deficiencies. Calcium deficiencies also appear to be accentuated by certain sources of N.

Detrimental effects from excess Ca seldom occur, but if they do these effects are likely to occur because of the accompanying anion or from Ca interactions with other elements like the induction of K and Mg deficiencies.

Magnesium

Compared to K, Mg accumulates in sorghum plants at relatively low concentrations (2 to 3 mg/g). Deficiencies of Mg seldom occur in plants grown on neutral to alkaline pH soils, but are common for plants grown on acid soils. Magnesium deficiencies may also be accentuated by available Al. Exchangeable sources of Mg appear to be made available to plants fairly easy, but even these sources of Mg may not be sufficient to meet plant needs at a particular stage of plant development. Soil solution Mg can vary widely with different soils (sands or clays) and with different soil parent materials. Levels of Mg in soil solutions between 2 to 5 mM are often reported. Magnesium deficiencies in soils are commonly alleviated when chromitic limestone is added. Both Ca and Mg are added with dolomite.

Like that of Ca, Mg is absorbed as a cation (Mg^{2+}), and this is the active form in metabolism. Magnesium is not readily complexed by organic compounds. The best known function of Mg is its occurrence in the chlorophyll molecule. The greatest proportion of Mg in plants (often over 70%) is diffusible and associated with the cytoplasm or vacuoles of cells. Magnesium is required in essentially all enzymes activating phosphorylation processes. As such, Mg is involved with phosphate and nucleotide transfer reactions. Magnesium is also associated with the stabilization and integrity of ribosomes and nucleic acids, and in the control of light-enhanced carbon dioxide (CO_2) fixation. Magnesium is fairly well distributed throughout the vegetative plant parts and about half of the plant Mg accumulated in kernels because of its high remobilization.

Plant growth usually decreases when Mg deficiencies occur, and the reproductive stage of plant development is usually delayed. Deficiency symptoms appear first on older leaves. Relatively large irregular necrotic spots or lesions appear uniformly on tips and margins and spread toward the base and midrib of the leaf. A characteristic plant symptom that often appears with Mg deficiency on many sorghum genotypes is a deep red color on leaves. Under severe Mg deficiency, large areas of necrosis develop, leaves become brittle, die and turn brown. Shoot/root ratios increase extensively with Mg deficiency, because Mg affects root growth much more than shoot growth.

Disorders from excess Mg seldom appear unless plants are grown on serpentine (high Mg) or distributed soils. High Mg can cause Ca, K and Mn deficiencies.

Sulfur

Relatively low amounts of S are required by sorghum and usually sufficient S is found in soils or added with other fertilizers (especially phosphates). Crops such as legumes have higher requirements for S, and if sorghum is in rotation or intercropped with some of these plants, residual soil S may be adequate to provide sorghum needs. Although both organic and inorganic forms of S occur in soils, organically bound S is the major reservoir. Since sulfate (SO_4^{2-}) is the form of S absorbed by plant roots, organic sources of S need to be converted to inorganic S before it is available for plant uptake and use. Under aerobic conditions, organic S is readily converted to inorganic S from microbial activity. Soils in arid conditions usually accumulate SO_4^{2-} , but SO_4^{2-} is easily leached in humid regions (acid soils).

Sorghum plant concentrations of S are about 1 to 2 mg/g. One of the important functions of S in plants is the formation of S-amino acids (cysteine, cystine and methionine) which are very important building blocks of proteins. These S-amino acids in proteins form disulfate bonds between polypeptide chains which maintain protein configuration through cross-bonding. Other S containing compounds vital to plant growth and development include Fe-S proteins, ferredoxin, lipoic acid, glutathione, biotin, thiamin and coenzyme A. Sulfur is relatively immobile and vegetative plant parts have comparable S concentrations. Kernels accumulate extensive amounts of S which is about half of the total plant S. The amount of S taken up with plant age follows closely that of dry matter accumulation.

Sulfur deficiencies can decrease plant growth and yield. Deficiency symptoms of S appear in the upper leaves and are more pronounced in the portion emerging from the whorl. Emerging leaves turn uniformly pale yellow. Sulfur deficiency is often indistinguishable from N deficiency, except that S deficiency occurs first in the upper leaves and N deficiency occurs first in lower leaves.

Disorders from excess S may occur because sulfur dioxide (SO_2) is a pollutant from many smelters and industrial plants burning fossil fuels. These S toxicities can occur at low levels of SO_2 . Disorders from excess S fed to roots are seldom reported since plants are relatively insensitive to SO_4^{2-} uptake. Because SO_4^{2-} is not readily absorbed by plant roots, disorders attributed to excess S may likely be due to its accompanying cation.

Manganese

Sorghum requires relatively low Mn concentrations for growth, and most soils usually contain more than adequate levels of Mn. The availability of Mn in soil may depend on factors like pH, moisture, microbial activity and organic matter which affect oxidation-reduction reactions. Total Mn levels of 200 to 3,000 $\mu\text{g/g}$ soil are common. As the availability of Mn becomes greater with increased H⁺ (lower pH), acid soil may contain relatively high available Mn which may be toxic to plants.

Manganese is absorbed as Mn_2^+ and this is the active form in plants. Manganese concentrations in plants vary, but are usually between 30 to 100 $\mu\text{g/g}$. The functions of Mn resemble those of Mg. Manganese may substitute for Mg in some

enzyme reactions, but in others Mn is more specific than Mg. Examples of these are decarboxylases and dehydrogenases of the tricarboxylic acid cycle. The oxidation of indolacetic acid has also been linked to specific Mn reactions. A major reaction specific for Mn is Photosystem II (photolysis of water) where Mn is essential in electron transfer. Manganese accumulates in metabolically active vegetative tissues (mostly in leaves), is fairly mobile in plants and about one-fourth of total plant Mn accumulates in kernels. Most Mn is taken up in plants by the early grainfilling stage.

Manganese deficiency is seldom a problem in sorghum, but when it is, plant growth and development are depressed. Manganese deficiency symptoms appear first in younger leaves. Leaves show a slight pale color in a streaked pattern in the interveinal tissue. In more severe Mn deficiency condition, long narrow lesions appear on leaves and each lesion is separated by veins. Portions of leaves, particularly the middle, may exhibit Mn deficiency symptoms and other portions will appear normal; leaves may bend or break at this point on the leaf. Shoot/root ratios tend to increase with Mn deficiency.

Disorders of excess Mn may occur on plants grown on acid and tropical soils or under flooded conditions. Fairly uniform small dark purple dots or flecks appear on leaves that otherwise remain dark green. In several cases, fairly long white (bleached) streaks or large sections of leaves may become white. Excess Mn can also cause Ca, K and Mg deficiency in leaves.

IRON

Soils generally contain very high amounts of Fe compared to the amount required for plant growth. Soluble Fe in alkaline and calcareous soils is normally so low that insufficient amounts are available for plant uptake and use. The equilibrium of Fe changes by 1000-fold; soluble Fe increases with lower pH (H^+ increase). Like that of Mn, Fe may also become toxic to plants grown on acid soils.

Of the 2 major ionic forms of Fe, ferrous (Fe^{2+}) is the form absorbed by plants, and most Fe in soils exists in the unavailable or insoluble ferric (Fe^{3+}) form. Since the major function of Fe in plants is associated with electron transport, both forms of Fe occur in proteins that contains Fe. Iron is also involved in chlorophyll synthesis and as a catalyst of a few enzymes (e.g., aconitase).

Iron-containing enzymes include cytochromes, catalase, peroxidase, superoxide dismutase and nitrite reductase. Important Fe compounds include Fe-S proteins, ferredoxin, and phytoferretin. Iron accumulates extensively in leaves, but roots contain even higher concentrations than leaves, often 5- to 10-fold higher. Iron is relatively immobile in plants, and only small amounts of Fe accumulate in kernels.

Sorghum is very susceptible to Fe deficiency chlorosis (often called "lime-induced chlorosis") when grown on many alkaline, calcareous soils. Whole fields or large areas within fields are commonly seen with Fe deficiency chlorosis. Since Fe in neutral or higher pH soils is usually insoluble, soil amendments or foliar sprays are added regularly to sorghum grown on these soils. Sorghum may require as many as 4 to 6 spray applications per crop during the vegetative growth cycle while soil amendments are usually good for only 1 or 2 crops. Even without foliar or soil amendments of Fe, sorghum plants usually regreen in the field as the

season advances and a harvestable crop is normally produced. Shoot/root ratio of plants remain fairly constant with Fe deficiency. Plant growth is reduced as long as relatively severe chlorosis persists. Plant maturity is delayed when plants persist in the chlorotic state.

Even though the first 2 or 3 leaves seldom show symptoms, Fe deficiency chlorosis appears first in newly emerging or younger leaves. Interveneal tissue of leaves turn pale yellow (chlorosis) with green veins. The chlorotic pattern is distributed fairly uniform over the length and breadth of the leaf. Under severe Fe deficiencies, leaves will turn completely yellow or even white and eventually die and turn brown unless corrective measures are taken.

Disorders from excess Fe can cause deficiencies of Mn, Cu, and Zn.

Boron

Sorghum plants containing deficient B concentrations have seldom been reported. Soils usually contain the low amounts of B required by sorghum, but under special conditions B deficiencies can occur in other kinds of plants (legumes and the brassicas). Some soils are formed from parent materials containing high B. Boron may be added to soils through irrigation with waters containing high B.

Boron is absorbed by plants as borate (BO_3^{3-}). Since B forms polyhydric compounds, the biochemistry of B is complex and elusive. Boron has been shown to be essential for many plant organisms, but has not been proven to be essential for all plants. A common feature of B deficient plants is the disturbance to and the poor development of meristematic tissues. Although the mechanisms for these disorders are not known. Boron has been shown to be required for the synthesis of nucleic acid compounds like uracil, which are essential components of ribonucleic acid (RNA) and deoxyribonucleic acid (DNA). Without these nucleic acids, the essential functions of cells in processes like protein synthesis, sugar metabolism and cell division are inhibited. Boron has also been associated with pollen tube growth and hormone (cytokinin) synthesis. If B deficiencies occur, newly developing meristematic tissues would be affected. In plants where B deficiencies occur, apical growing points stop developing, leaves may become thick, are often brittle and sometimes contain irregular chlorosis.

Boron toxicity may occur at relatively low concentrations. Of all elements required for plant growth, B has the narrowest concentration range between deficiency and toxicity. Boron toxicity can greatly reduce growth and occurs in tissues that transpire large amounts of water. Boron toxicity symptoms appear at the margins and tips of leaves, and a sharp demarcation between the light brown (strawcolored) affected tissue and the dark green unaffected tissue can be observed.

Copper

Copper deficiencies have occurred in plants grown on certain acid soils and have been reported for plants grown on many Australian soils. Soil solution concentrations of Cu range from 0.01 to 0.6 μM . Copper is associated extensively with organic matter and deficiencies occur most often in soils that contain high humus.

Copper is absorbed by plants as Cu^{2+} and accumulates in concentrations of up to 15 $\mu\text{g/g}$. Major functions of Cu in plants are with enzymes connected with

electron transport (cytochrome oxidase, laccase, ascorbic acid oxidase and polyphenol oxidase). Disruptions of desaturation and hydroxylation of fatty acids, and protein and carbohydrate metabolism have been associated with Cu deficiencies. Copper is also a constituent of superoxide dismutase, an enzyme that detoxifies superoxide radicals (produced from oxygen) which are very detrimental to cells. Copper is remobilized to some extent, accumulates evenly in vegetative tissues, and accumulates to some extent in kernels. Most Cu is taken up into sorghum plants by the early grain fill stage.

Copper deficiencies do not appear frequently in sorghum, but when they do, the younger leaf tips turn brown, roll up and break over. In many respects, Cu deficiency resembles Ca deficiency and symptoms may be Ca deficiency since Ca leaf tips is reduced with Cu deficiency.

Excess Cu can induce symptoms similar to Fe deficiency which are more accentuated near the base of leaves than in the apical portion of leaves.

Zinc

Zinc deficiencies may appear in plants grown on both acid and alkaline soils. Zinc deficiencies are often noted on sandy soils and on scraped or distributed soils. Zinc solubility and mobility is very low in high pH soils, especially when carbonate is present. Zinc levels are low in soils (10 to 300 $\mu\text{g/g}$) and soil solutions vary between 0.03 to 3 μM . Zinc absorbed by plants is in the cationic (Zn^{2+}) form. Zinc concentrations in vegetative plants are fairly consistent and range from about 20 to 40 $\mu\text{g/g}$.

Zinc is a component of the enzymes carbonic anhydrase, glutamic acid dehydrogenase, lactic acid dehydrogenase, superoxide dismutase, and some peptidases and proteinases. Zinc has also been found to be a precursor to auxin synthesis, in RNA stability and synthesis, and in starch formation. Zinc is not readily mobile in plants, and kernels accumulate relatively high amounts of Zn. Most Zn in sorghum is taken up by the early grain fill stage. Shoot/root ratios usually decrease slightly with Zn deficiency.

Zinc deficiencies occur first in the younger leaves. Emerging leaves become uniformly pale green to yellow with chlorosis starting at the base and progressing toward the tip. Leaf margins may show a distinct red line. Under severe conditions, Zn deficiency may be expressed as bleached white patches on the leaves.

Zinc excesses seldom occur, but when they do, leaves have a fairly uniform pale green color with slight streaking. Fairly long dark brown lesions form intermittently in the interveinal tissue.

Molybdenum

Molybdenum deficiencies often occur in plants grown on acid soils. Molybdenum is fixed by soil particles similarly to P and is next to P in strength of binding by soil minerals. Solubility of Mo increases with increasing pH. Mo deficiency can often be controlled by liming or raising the soil pH. Soil concentrations of Mo are usually well below 1 $\mu\text{g/g}$ for many soils.

Molybdenum is taken up as MoO_4^{2-} and accumulates in sorghum plants at concentrations below 1 $\mu\text{g/g}$. Molybdenum is a constituent of nitrate reductase, nitrogenase, sulfite oxidase, xanthine oxidase and reductase, and aldehyde oxidase.

Of these enzymes, only nitrate reductase has been found to be a true constituent of plants, while the other enzymes have been found in microorganisms associated with plants, particularly those associated with atmospheric N fixation. Molybdenum accumulation in kernels is usually low, but often sufficient to support the plant throughout its entire growth cycle after germination.

Molybdenum deficiency has not been reported in sorghum, but many reports of Mo deficiency in maize have been noted. Deficiency symptoms of Mo in maize appear in newly developing leaves similar to Ca and Cu deficiency. Leaf tips usually become slightly chlorotic than flaccid, become water-soaked, turn brown, curl, and often break over.

Plants can tolerate high levels of Mo without detrimental effects. When Mo excess occurs, symptoms are indistinguishable from P deficiency (uniform dark reddening over the leaf) symptoms.

OTHER ELEMENTS

Aluminum

Although aluminum (Al) has not been found to be essential for plant growth, beneficial effects of low Al has been reported. Beneficial effects of Al have been attributed to the solubilization of other elements, prevention of some other element toxicities, promotion of P uptake, prevention of P excess, delaying root deterioration by slowing growth and serving as a fungicide.

Aluminum toxicity is a common problem for sorghum grown on acid soils. Plants grow fairly well in soils with pH 5.0 to 5.5, and Al toxicities are minimal. Aluminum toxicities are usually alleviated by reducing available or exchangeable Al with the addition of lime or P. Lime is a very effective means for alleviating Al toxicities in soils. When Al is taken up it is likely absorbed as a cation (Al^{3+}), but hydroxyl forms of Al are often reported in soils. Aluminum can accumulate in and on sorghum roots at relatively high concentrations ($> 1,000 \mu g/g$), but Al is not easily translocated to leaves. Therefore, Al does not accumulate in kernels.

Toxic effects of Al are observed extensively on roots. Roots turn dark black or purple, are short, thick, often coralloid, low branching and brittle. Adventitious roots are often initiated to compensate for affected seminal roots, but Al affects auxiliary roots similarly. Iron, P, Ca, and Mg deficiencies may be induced by Al, and these deficiencies have been noted on sorghum leaves when grown with Al. The type of symptomology on leaves from high Al is often genotype-specific, but Fe, Mg, P and Ca deficiencies have been noted. Reduced growth and poor rooting patterns are common symptoms of Al toxicity on field-grown plants. Shoot/root ratios increase dramatically with Al toxicity.

Sodium

Sodium (Na) may accumulate to fairly high levels in saline soils. Even though Na is not required for sorghum growth, it is beneficial to some plant species. Sodium is a monovalent cation (Na^+) and may replace K^+ to some extent in plant metabolic and osmoregulatory reactions. Sodium usually accumulates in vegetative tissue and little goes to the kernels. Excess Na causes toxicity disorders. Symptoms appear first on younger leaves. The margins and tips of leaves turn flaccid and die. The remainder of the leaf turns pale, and distinct boundaries appear between

the flaccid margin and other portions of the leaf.

Chlorine

Like that of Na, chlorine (Cl) accumulates in saline soils. Chlorine is absorbed by Cl⁻, is required in photosystem II of photosynthesis and acts in neutralization and osmoregulatory processes. Chlorine may accumulate extensively in vegetative tissues, but little goes to the kernels. Chlorine excess is similar to and difficult to distinguish from Na excess; the leaf tips and margins wilt, turn brown, and die. Heavily transpiring leaves may be detrimentally affected by excess Cl.

Silicon

Silicon (Si) is the second most abundant element (next to oxygen) in the lithosphere and in soils. The accessibility of Si to plants is dependant on the weathering processes in soils. Acid soils usually contain higher concentrations of soluble Si than higher pH soils, but highly acid soils (pH < 4.5) may contain relatively little Si.

Although Si has not been found to be essential to plant growth, some beneficial effects of Si have been noted. Silicon has been reported to enhance stalk strength and mechanical stability of cells, to better protect plants from parasitic fungi and bacteria attacks and to promote reproductive organs (especially in rice). Silicic acid appears to form hydroxyl groups similar to those of P and B and can condense with sugars, alcohols and organic acids. Silicon may be able to replace, interact or interfere with P and B nutritional processes.

Silicon in sorghum leaves has been found to accumulate at fairly high concentrations (usually 20 to 30 mg/g), but over 50 mg/g has been noted. High Si accumulation in sorghum plants grown on limed acid soils and in plants grown on alkaline soils. Concentrations of Si in leaves of sorghum plants grown on acid soils (pH 4.2) were near 5 mg/g. Even though information on the function of Si in plants is limited, Si has been reported to cause a better distribution of Mn in plants and help alleviate Mn toxicity.

Excess Si causes sorghum leaves to become pale and younger leaves are affected more than older leaves.

Barium, Cadmium, Chromium, Cobalt, Lead, Mercury, Nickel, and Selenium

The essentiality of these elements in plants has not been established, and beneficial effects from some have been reported. For example, cobalt (Co) has been found in the cobamide coenzyme of microorganisms associated with atmospheric N fixation in plants; nickel (Ni) has been reported as a component of urease in some plants; chromium (Cr) has been found to participate in glucose metabolism, especially mammals; selenium (Se) may replace S in some plant reactions; cadmium (Cd) seems to mimic Zn in some processes; and strontium (Sr) and Ca chemistry appear to be similar. Most of these elements are toxic to plants at relatively low concentrations. Toxicity symptoms for each of these elements in sorghum have been noted:

Barium

Dark red lesions with lighter color near the margins progressing toward the midrib; symptoms were more severe from the whorl toward the tip. Roots had no

secondary root lengthening and were dark in color.

Cadmium

Leaves turned a fiery red from margin to midrib; severely affected, they became bright red over the entire leaf. Roots were dark red, small, and had no growth on secondary roots.

Chromium

Leaves turned light reddish-brown from tip toward base and from margin to midrib. Some leaves had somewhat dark reddening on tips and margins. Roots were darker and stubbier and growth was inhibited extensively.

Cobalt

Leaves had symptoms similar to Fe deficiency, except that the symptoms appeared only in the leaf just emerging from the whorl or on the sheath next to the whorl and not in the leaf tip sections. The symptoms were more diffuse than those typical of Fe deficiency. Roots showed some stubbiness.

Lead

Leaves turned reddish-brown and had necrotic dead spots with red around them. Leaf tips were affected more than the leaf base and symptom severity progressed from margin to midrib. Roots were stubbier and had fewer auxiliary roots, but were normal than roots grown with Cd.

Mercury

Leaves turned blackish-brown with dark and necrotic lesions. Leaves wilted and became water-soaker, were leathery, and curled extensively. Leaves did not turn lighter in color. Roots were somewhat inhibited in growth, but otherwise were relatively normal.

Nickel


Leaf symptoms were similar to Fe deficiency. These symptoms did not extend as far out toward the leaf tip as noted for typical Fe deficiency. Roots were stubbier and showed symptoms resembling those of excess Al, but not as severe.

Selenium

Leaves showed symptoms that were indistinguishable from Mo excess which were similar to P deficiency. Roots showed no abnormal symptoms with excess Se.

Strontium

Leaves became necrotic in a spotchy pattern at the margins with a lighter color appearing in the margin progressing toward the midrib. Roots were dark red, coarse, stubby and somewhat slimy.



IMPROVEMENT OF CROPS: THE ROLE OF MORPHOPHYSIOLOGICAL TRAITS

INTRODUCTION

The productivity of a crop depends on the efficiency with which morphophysiological traits manifest themselves in diverse environments. To date, breeding criteria for sorghum have largely been on the basis of morphological characteristics, and very little attention has been paid to physiological traits. Because of the synthesis of crop growth and development in sorghum, the author urges plant breeders to modify their approach to increase productivity in diverse environments and breed cultivars adaptable to them. Identification of traits related to several abiotic and biotic stress factors affecting stages of crop development is desirable, and these need to be taken into account of any crop improvement program.

To formulate an efficient breeding program, breeders need to study the genetic variability of different traits in existing germplasm and breed materials of the crop to be investigated. Through different selection procedures they will identify a particular plant type or trait pertaining to yield and other desirable qualities, and use them in different crossing programs after establishing their purity. A wide range of genetic variability and genotypes showing the stability of yield under diverse climatic conditions are utilized by adopting suitable breeding techniques for a particular crop.

To formulate an efficient breeding program, it is desirable to identify morphophysiological traits related to resistance and yield, and search for variability of these traits existing in sorghum germplasms and incorporate them into elite breeding lines. Morphophysiological traits existing in sorghum germplasm and offering great scope of selection have been discussed in earlier chapters, and some techniques for their evaluation and probable role in sorghum crop improvement have already been described.

Grain yields in sorghum have substantially increased with the use of high-yielding, management-responsive F1 hybrids and varieties, but these cultivars have miserably failed under adverse conditions prevailing in the SAT. Therefore, we should be aware of the problems that farmers face and test improved farming techniques before suggesting their adoption. Better agronomic practices and use of improved cultivars have significantly contributed to the enhancement of sorghum yields. Though the degree of improvement accomplished so far has been high, there is ample scope for increasing production by improving genetic stock and breeding material. In order to accelerate progress towards better yields, there

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is a need to promote the collection, conservation, evaluation and utilization of germplasms for different traits which will improve crop productivity.

This chapter presents a brief summary of the development of simple techniques and their utilization in the identification of stress factors at various stages of plant development in sorghum. It discusses in some detail the morphophysiological traits related to plant productivity under optimum and adverse conditions, selection of techniques for evaluation of germplasms and elite lines for multistress resistance and some hypotheses. It also discusses the need to simultaneously incorporate several traits into elite breeding stocks and gain better understanding of the plant-environment relationships to deal with these problems.

Sorghum crops in SAT environments face different biotic and abiotic stress factors at different stages of crop development. There is a necessity to select genotypes resistant to stress factors that affect the sorghum crop in these environments. Having determined the range of variability in morphology and growth patterns in diverse environments, several research requirements come into focus. In this chapter, problems occurring at different stages of crop development and productivity are identified.

SEED CHARACTERISTICS AND SEEDLING ESTABLISHMENT

There is great diversity in seed morphological characteristics and good correlation exists among different morphological and physiological characteristics of sorghum at seed and early seedling establishment stages. For example, seed size and first leaf area are found to correlate with good emergence and high seedling vigor. Therefore, selection for better stand establishment on the basis of seed morphological and physiological traits is possible.

Poor stands are one of principal causes for low yields in SAT. Several stress factors are responsible for this. Here are a few examples of how sorghum germplasm could be screened for several stress factors.

Seed viability following wetting and drying

Some sorghums genotypes retain their viability even after germinated seeds were subjected to a dry spell. This is an important desirable characteristic in dry sowing where a small shower will not affect seed viability. A number of viable genotypes have been identified which should be tested in dry sowing environments. In the light of the earlier literature, it is expected that lines selected for this stress may be resistant to water stress. Biochemical characteristics related to resistance to this stress factor need to be investigated.

Grain quality, germinability and dormancy

Lack of high seed quality is one of the major causes for poor emergence. The environment and season in which seed is produced affect seed quality to a great extent. Infestation of grain with mold and preharvest germinability during the rainy season causes grain deterioration in sorghum. Early germinability causes hydrolysis of starch in the grain which encourages the growth of saprophytic fungus, thereby causing further deterioration of grain quality. This causes poor emergence and

poor seedling vigor in sorghum. Techniques have been developed and lines have been identified for these genetic and biotic stress factors, viz. resistance to preharvest sprouting and grain mold. Dormancy of grain during and after maturation reduces grain weathering and improves grain quality.

Sorghum genotypes vary widely for germinability at early and late stages of grain development. This has a direct impact on grain weathering and quality during the rainy season. There is much variation in mold development at different stages of grain development. Some genotypes with less germinability and less mold infestation at major stages of grainfilling were identified. These lines should be tested in a grain mold nursery for effective selection. More research needs to be directed to select lines resistant to preharvest sprouting and grain mold.

Seedling emergence and seedling vigor

Several management and biotic factors like depth of planting, soil temperature, soil crusting and compaction, poor vigor and susceptibility to water stress at the seedling stage, cause poor emergence and seedling. Extensive research has been undertaken to understand these stress factors and select lines resistant to individual stress. In the process, we may also discover genotypes showing multiple resistance.

Initially, major attention needs to be paid to improve grain quality. Genotypes could then be selected for better grain characteristics like large seed size, large embryonic area, first leaf area, and good grain quality with high protein content. Genotypes thus selected could be tested for better performance under adverse situations like emergence from deeper depth of planting, high soil surface temperature, crust and compaction and seedling growth under water stress. Consequently, lines could be selected that are resistant to stress factors.

Several morphological traits related to resistance to stress factors could be identified. For example, rapid mesocotyl and coleoptile elongation are found related to better emergence from deeper depths of planting. There are reports that long coleoptile and large coleoptile cross-sectional area are associated with better emergence through soil crust and compaction. Genotypes showing high seedling vigor show better emergence through soil crust and are also tolerant to water stress at the seedling stage. Again, genotypes showing glossy leaf characteristics at the seedling stage show good tolerance to water stress and several insects. Genotypes resistant to drought at the seedling stage are also resistant at the adult growth stage.

Research needs

Seed characteristics

1. Identification of seed morphological characteristics linked with seedling development/yield attributes or host resistance to insects/diseases.
2. Determination of the relationships between certain characteristics like grain hardness, corneous endosperm content, water uptake, grain cooking quality and disease resistance traits.
3. Identification of drought resistant genotypes which show maximum seed viability.
4. Categorization of genotypes with different ranges of germinability and screening these for resistance to grain molds.

Selection for seedling vigor

1. Identification of high vigor lines with good agronomic attributes from germplasm and breeding lines.
2. Heritability of seedling vigor in high X low, high X high using the regression method.
3. Performance of high vigor lines under favorable and unfavorable conditions viz. crusted, low phosphate, low and high fertility, saline soils and under different depths of planting and kinds of weed competition.
4. Relationship between elongation of the primary root, emergence of secondary roots and crop establishment.
5. Utilization of high vigor lines in crossing with standard breeding lines for yield improvement using pedigree selection.
6. Mobilization efficiency of seed reserves of the lines showing emergence from deeper depth and high vigor needs.

Emergence through crust

1. Standardization of techniques using perfos and sprinklers.
 2. Identification of lines with good emergence ability and determination of the causal factors responsible for better emergence.
 3. Identification of lines with good agronomic traits.
 4. Study of the resistance mechanism that inhibits emergence through crust.
- Standardization of techniques for drought resistance at seedling stage 1

Germination

1. Germination under carbowax (polyethylene glycol) induced stress.
2. Germination and emergence under moisture stress.

Tolerance of stress by the seedlings

1. In cylinders.
2. In wooden flats/brick flats.
3. In field using perfos and sprinklers.
4. Assessing the relative efficiency of the different techniques and their potential.
5. Correlation between laboratory and field experimentation.

Selection of lines resistant to drought and study of resistance mechanism

1. Identification of seedling drought-resistant lines with good agronomic attributes and identification of a marker for drought tolerance.
2. Survey of world germplasm in order to locate the geographical distribution of resistant lines and their taxonomic status.
3. Mechanism of drought resistance: i- seedling roots, ii- anatomical structure in relation to water use efficiency, iii- scanning microphotographical examination of epidermis and wax, and iv- physical and biochemical studies of resistant and susceptible genotypes.
4. Inheritance and heritability of seedling drought tolerance in resistant X susceptible crosses.
5. Performance of resistant lines and progenies under different conditions, i.e. crop establishment, depth of planting, moisture stress, and pest resistance (shootfly, shoot bugs, etc.).
6. Incorporation of drought resistance into male sterile lines by backcrossing if feasible.

Relationships between drought resistance at seedling stage with that at advanced stages: GS1, GS2 and GS3.

PANICLE DEVELOPMENT

The productivity of sorghum depends on the efficiency of panicle development and the influence of the environment on it. Drought directly affects the initiation of panicle (GS1), the development of spikelets, flowering and grain maturity.

Research has been undertaken on the effects of weather on panicle productivity and grain yield. For example, water stress delays panicle initiation, development of spikelet primordia, days to flowering, quickens the grainfilling period, but reduces grain size. Genotypes tolerant to unfavorable conditions in terms of panicle growth need to be selected and those showing less interrupted panicle growth under water stress could be selected for their resistance.

More investigation is needed on the effects of water stress factors and the effect of light intensity on the sequential development of panicle. Several unfavorable environmental conditions like lack of water, low light intensity and nutrient availability, high temperature, etc., drastically reduce the productivity of the panicle. Under these stress situations, crops are often prevented from expressing their full genetic potential. It is therefore necessary to study in detail the effect of different environmental components on panicle differentiation and productivity, and to determine the optimum and minimum of each component of panicle growth.

Under severe water stress, differentiation may be delayed but not suspended. This in turn causes reduction in floret number and affects pollen tube growth and grain development. No detailed studies have been undertaken on the developmental aspects of panicle growth and vegetative growth simultaneously.

In SAT, uncertainty of rainfall and fluctuations in weather continue to have a direct impact on crop yield potential. Studies indicate that the change in weather directly influences the growth stages in sorghum-panicle initiation (GS1), days to flowering, grainfilling period and crop maturity. This in turn influences partitioning and translocation of photosynthates in the source and sink, thereby influencing the yield potentials in sorghum. Translocation of photosynthates in grain also varied in different genotypes. It is necessary to select genotypes which translocate major part of the photosynthates into grain under normal and stress conditions.

Temperature plays an important role in determining growth stages. The effect of weather in growth stage modeling needs to be emphasised. Breeding of genotypes needs to be concentrated in a particular season for adaptation in that season.

Compact panicle in sorghum provides favorable environments for infestation of disease and insects in tropical climates. Lax panicles may be good under this situations. Therefore, a new sorghum ideotype should be formulated.

ROOT GROWTH AND DEVELOPMENT

Due to difficulties in the extraction of roots from the soil very little progress

has been made in root studies. Some simple techniques need to be evolved to facilitate root studies. More concerted research needs to be directed to the root systems as they play a vital part in plant growth and uptake of nutrients. The relationship between the seedling and the adult root system needs to be investigated. The seedling root system should also be studied both under water stress and nonstress situations. Efficiency of root elongation under water stress could be correlated to drought resistance. We need to assess whether seedling resistance could be correlated with the resistance at adult stage. If this hypothesis is confirmed, a large number of genotypes could be evaluated at the seedling stage for both under stress or nonstress situations and lines could be classified on the basis of the intensity of their root systems. Clipping treatment could be attempted to investigate this, as well as testing under artificial conditions by permitting only the desired member to grow.

Some anatomical characteristics like intensity of sclerenchyma in the root pericycle and silica particles in endodermis may be correlated with drought resistance. Research into the root systems indicates that more than 80% of the root mass is located in the upper 20-30 cm of the soil profile, thus it will be easier to extract and study the root system from the upper layer. Genotypes thus selected could be assessed later on for deeper root systems. Recombination of profuse root systems at the upper layer and a number of deeper roots may do well under water stress situation. However, simple techniques need to be developed to evaluate genotypes *vis-a-vis* their root systems.

The methodology for studying root growth and development is complicated. A brickchamber technique has been developed for root development studies at ICRISAT. This technique is capable of distinguishing genotypes in their pattern of root growth. The development of roots in brick chambers was almost similar to the one found in the field, and a sorghum hybrid CSH8 which showed some level of drought resistance under the field conditions produced a better root system (biomass) compared to V302, a drought susceptible cultivar. Comparative study of the phenology and root growth of sorghum cultivars in alfisol and vertisol was made in a brick chamber.

GLOSSY SORGHUM GERMPLASMS: STUDIES ON THE RESISTANCE TO BIOTIC AND ABIOTIC STRESSES (Maiti, 1991-92; sabbatical stay at ICRISAT)

World sorghum germplasm can be classified into 2 distinct morphological types, glossy and nonglossy, based on visual characteristics at the seedling stage. Out of 17,536 accessions observed only 495 were glossy, and although they originate from a wide geographic and taxonomic distribution, the majority came from the Indian penninsular region and from the taxonomic race Durra. Glossy lines show variability in seedling morphology, seedling vigor, leaf surface structure, physiological, biochemical and agronomic traits. They show multiple resistance to shootfly, stem borer and several other insects and abiotic stresses like drought, salinity, high temperature and nutrient uptake. Other characteristics include higher water use efficiency and better growth under water stress situation compared to nonglossy

lines. Therefore, glossy sorghums may serve as basic resistance sources and diverse gene pools for improving biotic and abiotic stress resistance. Sources of economical-useful traits were identified for future incorporation in the improved cultivar. Besides, sorghum germplasm with high glossy score can serve as an important source to improve forage and grain yield. Therefore, glossy sorghum germplasm associated with multiple resistances shows a wider genetic base for specific traits and can be explored in genetic improvement for the semiarid regions of the world.

Taxonomic groups and geographic distribution

Only 477 out of 495 glossy sorghum accessions were classified (Table 9.1). Glossy lines appear in all the basic races and intermediate races except Bicolor-Guinea and Bicolor-Kafir. While 10% of germplasm collections from India (Durra race) are glossy, only 2% from Nigeria and about 1.5% from USA have glossy trait. Glossy lines have a diverse geographic origin (Table 9.2). Durra sorghum of India are mostly from the drier central parts of the country where the existence of shootfly and drought resulted in expression of resistance to these condition by some sorghum lines (Maiti *et al.*, 1984).

Table 9.1 Taxonomic distribution of glossy lines in the world sorghum germplasm accessions evaluated at ICRISAT (Maiti *et al.*, 1984).

Taxonomic groups	# lines	Taxonomic groups	# lines
Durra	400	Caudatum	3
Durra-bicolor	31	Bicolor	2
Durra-caudatum	26	Guinea-caudatum	2
Guinea	8	Caudatum-bicolor	1
Durra-kafir	3	Durra-guinea	1
Total	477		

Table 9.2 Distribution of glossy lines by countries in the world germplasm collection evaluated at ICRISAT (Maiti *et al.*, 1984).

Origin	Total	Glossy (%)	Origin	Total	Glossy (%)
India	4027	417 (10.36)	Ethiopia	4113	3 (0.07)
Nigeria	1173	25 (2.13)	South Africa	659	2 (0.30)
U.S.A.	1867	24 (1.28)	Mexico	234	2 (0.36)
Sudan	2255	11 (0.48)	Kenya	761	1 (0.13)
Cameroun	1835	8 (0.43)	Uganda	612	1 (0.16)
Total	17356	495			

Characterization of glossy trait

Seedling morphology and vigor: Glossy lines are rare in sorghum germplasm: out of 17,536 lines observed, only 495 were found to possess the glossy trait, but 32,000 germplasm accessions have not been screened for glossiness.

Glossy lines have light yellow green leaves with a shiny surface appearance in sunlight. Nonglossy "normal" sorghum lines have dark green and generally broad and pendant leaves. Leaves may be broad, semibroad or narrow depending on genotypes. Seedlings in glossy lines are generally erect and leaves are stiff, but broad and slightly pendant leaves are also not uncommon. The time of appearance of glossiness differs among genotypes. In some, it may appear as early as the first day after seedling emergence, while in others as late as 10-15 days after emergence. Variation in soil fertilities have no effect on glossy expression (Maiti *et al.*, 1984). Traere *et al.* (1989) reported that some leaves may be nonglossy in the same line, but recent observations showed that all leaves in a glossy plant were glossy, but considerable variations in the intensity of glossiness has been observed. This variation can be quantified on a 1-5 scale (1 = most glossy, 4 = least glossy, 5 = nonglossy). Glossy lines also vary greatly in seedling vigor which is evaluated through a visual scoring method (1 = most vigorous and 5 = least vigorous; Maiti *et al.*, 1981).

Biophysical and biochemical distinction between glossy and nonglossy sorghum

Nonglossy lines have deep green and pendant leaves, while the glossy lines have light yellow-green and stiff leaves with shining leaf appearance at the seedling stage. The biochemical factors leading to visual differences between glossy and nonglossy lines are not yet known. The light yellow-green color of the glossy leaves may be related to the chlorophyll content and the shining (glossy) leaf surface to the epicuticular wax. The visual difference between glossy and non-glossy trait disappears at advanced seedling stages (Maiti *et al.*, 1991).

Chlorophyll

Genotypes with low chlorophyll a and b contents were reported to be resistant to shootfly (Mate *et al.*, 1988). Drought tolerance in sorghum is associated with an increased number of leaves and increased chlorophyll content (Hou *et al.*, 1987). High solar intensity increased the rate of synthesis of carotenoids, chlorophyll a and b in both unstressed and drought treatment (Masojidek *et al.*, 1991). Many variations in chlorophyll and epicuticular wax contents were observed among glossy lines at 20-day seedling stage (Maiti *et al.*, 1991). Chlorophyll contents of 6 glossy and 6 nonglossy lines are shown in Table 9.3.

Table 9.3 The mean values of chlorophyll content (mg/g) of glossy (G) and nonglossy (NG) sorghum lines at 7, 14 and 21 days after emergence (DAE).

DAE	Total chlorophyll		Chlorophyll a/b	
	G	NG	G	NG
7 days	2.61	3.22	1.63	2.04
14 days	2.61	3.22	2.57	2.35
21 days	3.73	3.65	1.78	1.84

Glossy and nonglossy sorghum genotypes did not show significant differences in chlorophyll content, but significant differences for these components were observed between stages (Figs. 9.1-9.3) and glossy lines (Fig. 9.4). Nonglossy lines did not show significant differences in these components (Table 9.4). Correlation analysis among sorghum genotypes at different stages showed that there were no significant correlations with chlorophyll content, whereas significant correlations ($P = 0.05$) were found among genotypes within the stage.

Table 9.4 Analysis of variance (F-ratio) of chlorophyll content (mg/g, fresh weight) (* $P = 0.05$).

Source of Variation	df	F-value		
		Chlorophyll a	Chlorophyll b	Chlorophyll (total)
Intervals	2	4.79 *	13.92 *	5.62 *
Glossy	5	2.85 *	3.10 *	3.12 *
N. glossy	5	0.55	1.08	0.67
Glossy vs N. glossy	1	0.50	0.51	0.54

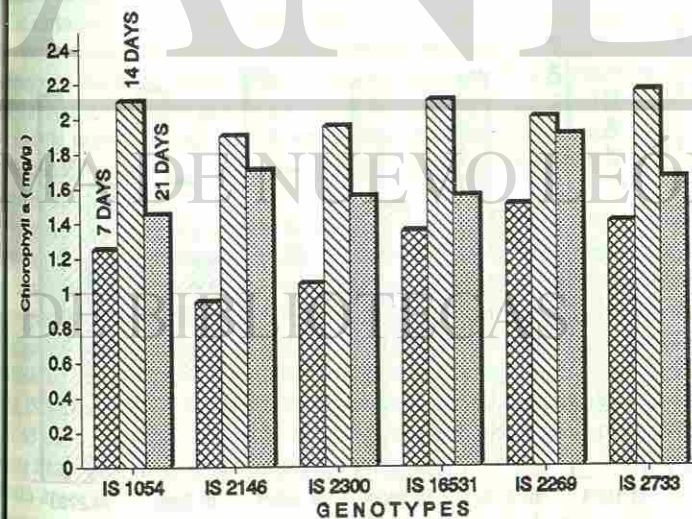


Figure 9.1 Chlorophyll a content in 6 glossy sorghum lines at 7, 14 and 21 days after emergence.

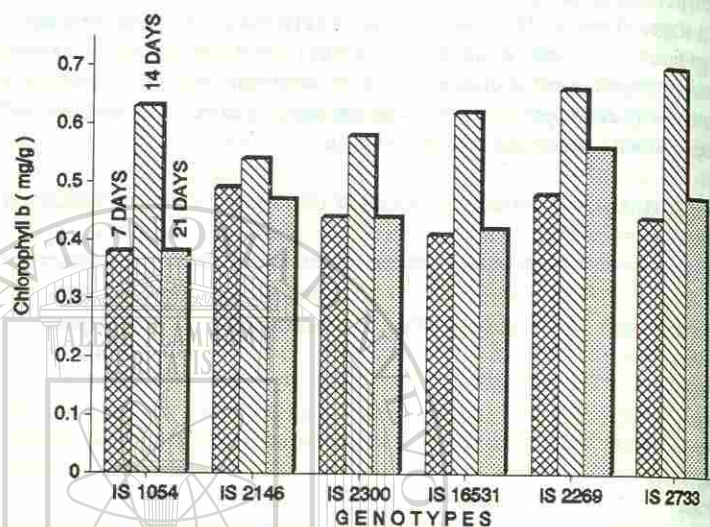


Figure 9.2 Chlorophyll b content in 6 glossy sorghum lines at 7, 14 and 21 days after emergence.

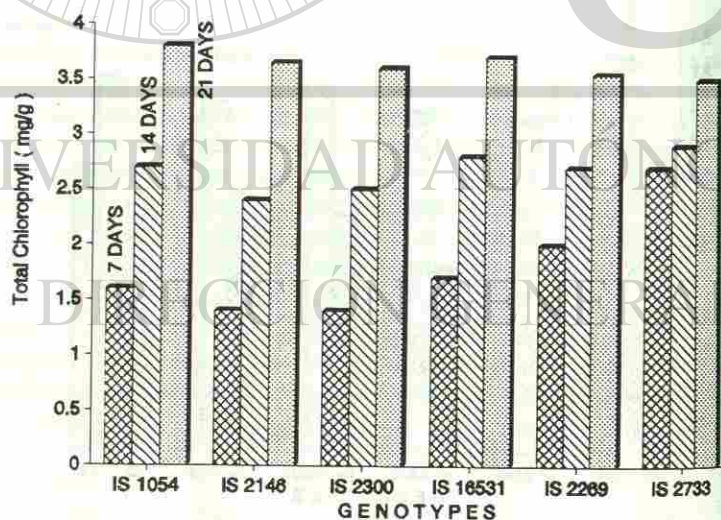


Figure 9.3 Total chlorophyll content in 6 glossy sorghum lines at 7, 14 and 21 days after emergence.

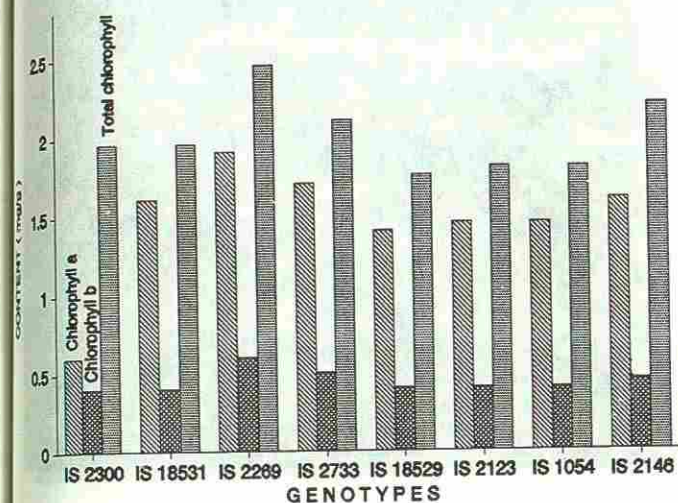


Figure 9.4 Chlorophyll content (a, b and total) at 21 days after emergence in glossy and nonglossy sorghum lines.

Epicuticular wax (EW) structure

EW may be related to insect resistance (Rodríguez *et al.*, 1983) and drought resistance at the seedling stage (Jordan, 1983; Jordan *et al.*, 1984).

The variations in the leaf surface epicuticular wax structure in a set of glossy sorghum lines were studied in order to find a possible relation to shootfly and drought resistance at seedling stage. Epicuticular wax structure of upper surface of fourth leaf (12 days after emergence) varied widely among glossy sorghum genotypes, including smooth waxy coating, coalescence wax, filamentous wax and wax plates. Epicuticular wax structure of lower surface of fourth leaf varied widely among genotypes. Filamentous wax was present in abundance.

The genotypes showed larger variations in epicuticular wax structure viz in the appearance of smooth shining surface, intensity of projected wax threads, its size and wax crystals. The presence of trichomes with sharp tips are prominent in some genotypes: IS 1054, IS 5282, IS 5567, and IS 2312. Variations in intensity and size of projected filamentous threads is prominent: in globular forms IS 2396, IS 5359, IS 5484, IS 5567, IS 8977; globular and short wax threads, IS 1054, IS 2205, IS 2312, IS 3962, IS 5484, IS 18390; long projected coiled threads, IS 1096, IS 4576, IS 4663, IS 5282. Wax filaments are oriented along the veins or epidermal cell walls arising from cork cells located on both sides of silica cells. All glossy lines have a smooth amorphous wax spreading over the entire leaf surface which causes the reflectance of sun rays thus imparting to the intensity of glossiness (Plates 9.1 & 9.2).

a)



b)

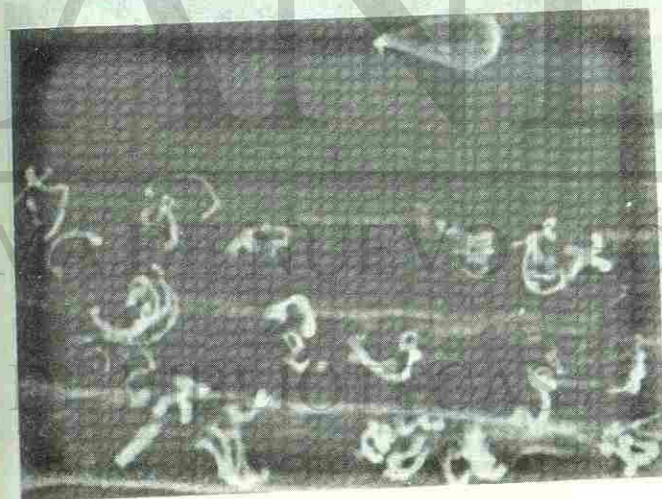
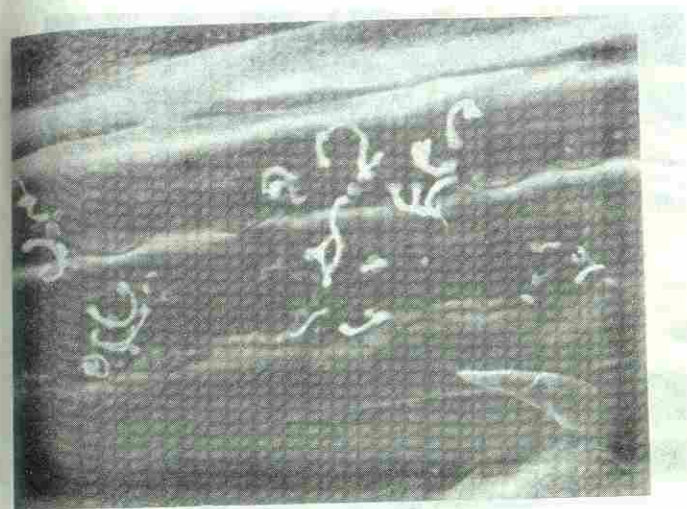


Plate 9.1 Variation in leaf surface structures in some glossy lines.
a) IS 4661; b) IS 5642 showing uneven surface and wax filament threads.

c) IS 5282; d) IS 2146 having smooth surface, nonglandular trichomes and wax filaments.

a)



b)

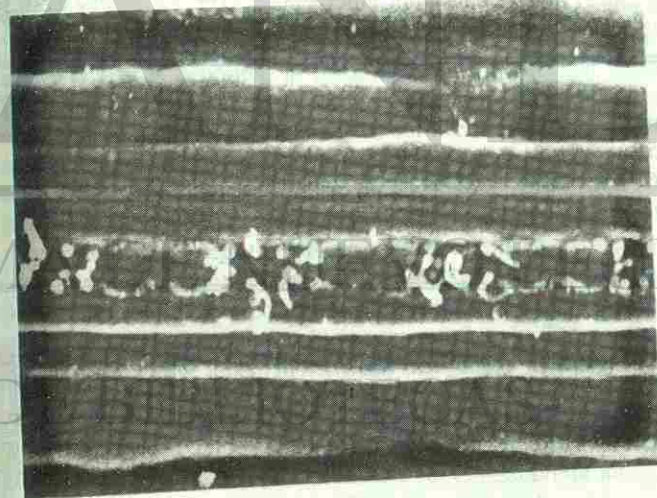
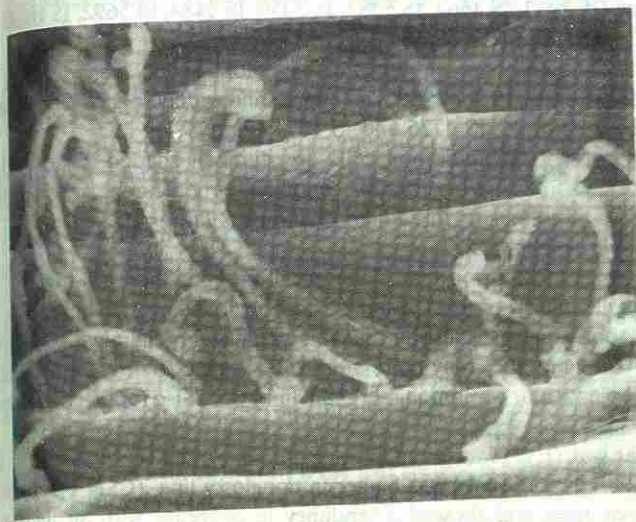


Plate 9.2 Variation in silica crystals and wax filaments projecting from the cells on both sides of silica crystals: a) IS 2205; IS 5622. IS 4776; d) IS 4473.

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On the basis of the scanning micrographs the genotypes may be classified as highly glossy (IS 1096, IS 2205, IS 2312, IS 2396, IS 4776, IS 5282, IS 5567, medium glossy (IS 3962, IS 4663, IS 5282, IS 5359, IS 5484, IS 5692, IS 18390 and less glossy (IS 4661, IS 5622, IS 5642).

The intensity of platelike wax crystals varied among genotypes viz., IS 4661, IS 18390, IS 5484, IS 5622, IS 5642; but was sparse and widely spaced as in IS 4663, IS 5484, IS 2312, IS 2396, IS 4776 and IS 1054 (Plate 9.2).

Silica cells present on epidermal cells are dumbbell shaped, bi- or trilobed varying in size and intensity in different genotypes. These are covered partially or heavily with amorphous or threadlike filaments (Plate 9.2).

Epicuticular wax content

Maiti *et al.* (1991) reported that glossy sorghum lines show variability in the contents of epicuticular wax, total, a and b chlorophyll and hydrocyanic acid at the seedling and adult stages suggesting that this variation in chemical components among glossy sorghum lines may be related to resistance to drought and insects. Variability in epicuticular wax among sorghum lines were also reported by Ebercon *et al.* (1977).

Epicuticular wax (EW) was found in trace amounts in all genotypes at 7th day. At 14th and 28th days the EW was higher in nonglossy line, (CSH 1), compared to that in glossy lines and showed a tendency to decrease with an increase in glossiness intensity (Table 9.5).

Table 9.5 Epicuticular wax content (EW/cm² leaf area) of 4 sorghum genotypes at 7, 14, 21 and 28 days after emergence (Score 1 = Highly glossy, 3 = Intermediate, 5 = Non-glossy).

Genotype	Score	Days after emergence			
		7	14	21	28
IS 18551	1	Trace	0.020	0.042	0.029
IS 1046	3	Trace	0.018	0.020	0.019
IS 1054	4	Trace	0.015	0.024	0.022
CSH1	5	Trace	0.025	0.032	0.032

The results show that the chlorophyll contents were slightly higher in nonglossy lines, but were significantly different among seedling stages for chlorophyll a, b and total. Therefore, the higher chlorophyll contents in nonglossy lines is responsible for imparting their dark green leaf color. This result coincides with the observation of García-Mendoza (1986) that nonglossy lines had higher chlorophyll content compared to glossy ones. The difference in chlorophyll content between glossy and nonglossy lines were reduced at advanced seedling stage.

Epicuticular wax structure

The reflectance of sorghum leaves at 500-2000 nm was found to vary with epicuticular wax content (Blum, 1975a), and their glossy appearance was found to be related to epidermal hairiness and degree of wax deposition (Traere *et al.*,

1989). The glossy appearance of the leaf was estimated by visual scoring or by observing sprayed water droplets under bright light (Maiti *et al.*, 1984; Traere *et al.*, 1989). The nature of the structure present on the leaf surfaces of sorghum genotypes varying in glossiness and their optical properties were studied. The genotypes used in the study had different glossy intensity: IS 18551 (1), IS 1046 (3), IS 1054 (4) and CSH 1 (5).

A comparison of micrographs before and after dewaxing revealed the presence of epidermal structures in all genotypes with variation in density. The aggregation of epidermal structures after dewaxing could be due to epidermal deformation as a result of chloroform treatment. These observations clearly demonstrate the possibility of the presence of epidermal structures which were not affected by organic solvents that look like alveolar material with waxlike appearance. The density of these epidermal structures decreased with the intensity of glossiness. (Plates 9.3 & 9.4).

It is possible to explain the difference in glossiness of various genotypes irrespective of the amount of the epicuticular wax content. When light falls on a relatively smooth leaf surface the wave length of the reflected light depends on the pigments in the leaf. However, if the leaf surface is rough it acts as a diffuser thus resulting in a uniform white appearance of the leaf surface together with the reflected wave lengths characteristics to leaf pigments. Thus glossiness is inversely related to the roughness of the leaf surface. Glossy leaves show higher reflectance and transmittance of light compared to nonglossy ones.

No specific relationship has been observed in EW content between glossy and nonglossy lines. Trace levels of EW were detected at the early seedling stages (7th day), but EW was higher in nonglossy lines compared to glossy ones at 14th day. It seems that EW is deposited in thick layer on the cuticular surface of the nonglossy lines and thin layers on glossy lines. Therefore, it is assumed that the presence of a thin film of EW on the cuticular surface in glossy lines contributes to shining appearance. More studies are needed for confirmation.

Differential resonance activity between glossy and nonglossy lines

Epicuticular substances, probably smooth waxy coating on glossy leaf surface, offer resistance to the penetration of light causing less resonance units without any change even at higher wave lengths. In the case of nonglossy lines, this substance is absent causing easy penetration of the wave length of light and higher excitation of cytoplasmic materials resulting in higher resonance units. These units decreased with an increase in wave length in nonglossy lines unlike that in glossy ones (Fig. 9.5; unpublished).

Variability in morphological, anatomical and biochemical characters

Epidermal trichomes: Many of the glossy lines possessed microscopic hairs (trichomes) on both sides of their leaf surfaces (Maiti and Bidinger, 1979). The trichomes are frequently pointed at the tip. The size and morphology of the trichomes differ from genotype to genotype (Maiti *et al.*, 1980). They are directed towards the base, with more of them on the upper than on the lower surface (Plates 9.5 & 9.6).

The density of trichomes on the leaf surface is highly variable, being maximum towards the tip, less at the base and intermediate at the mid portion. The trichome length varies from 20 to 55 μm (Maiti *et al.*, 1980).

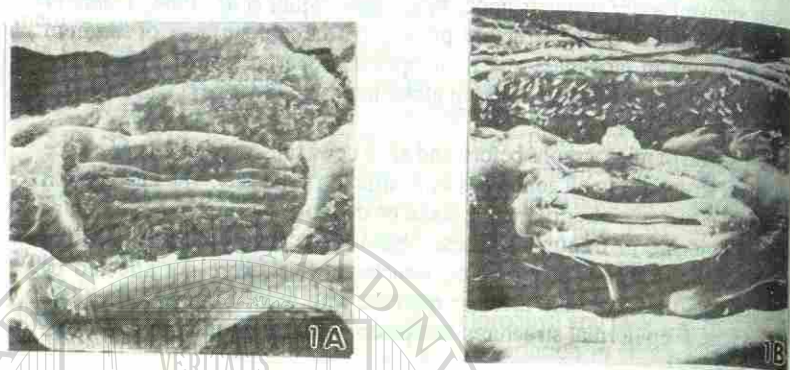


Plate 9.3 Scanning electron micrographs of adaxial surfaces of 4th leaves (suffices A and B refer to After and Before dewaxing): 1A/B) IS18551

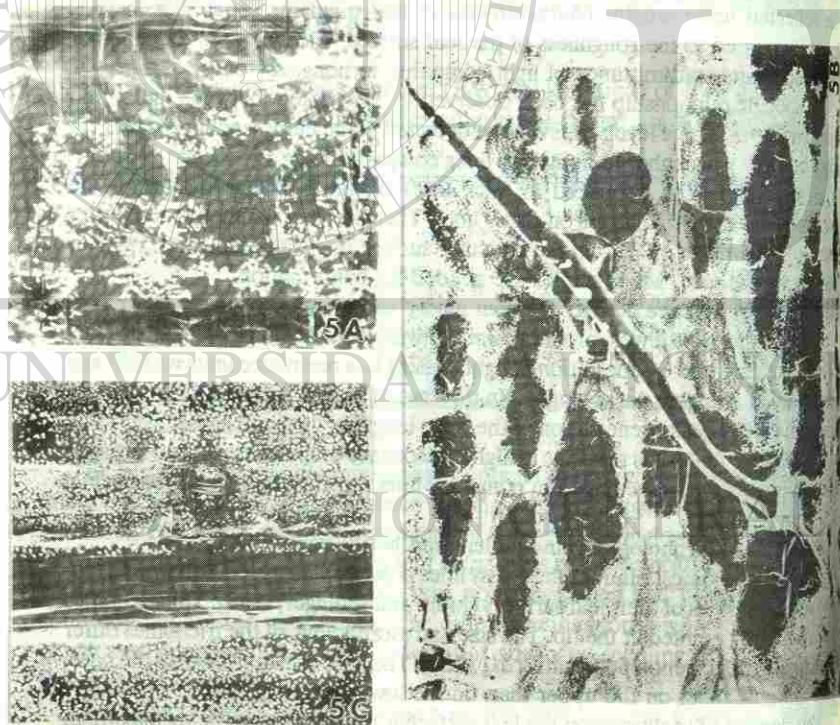
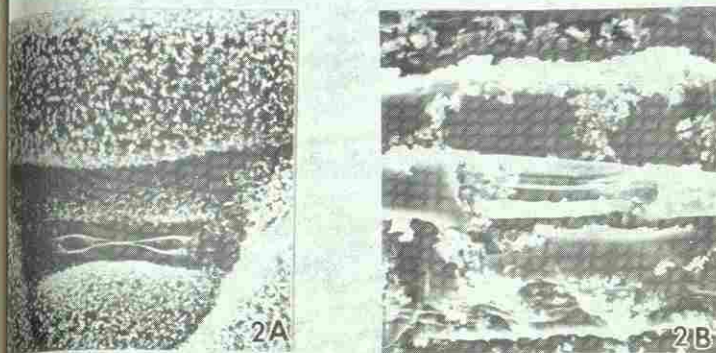


Plate 9.4 Sorghum CSH1: 5A) Sheath segment of 2 leaf (3rd leaf stage); 5B) Leaf lamina close to junction. 5C) Sheath segment after dewaxing.



2A) IS 1046.

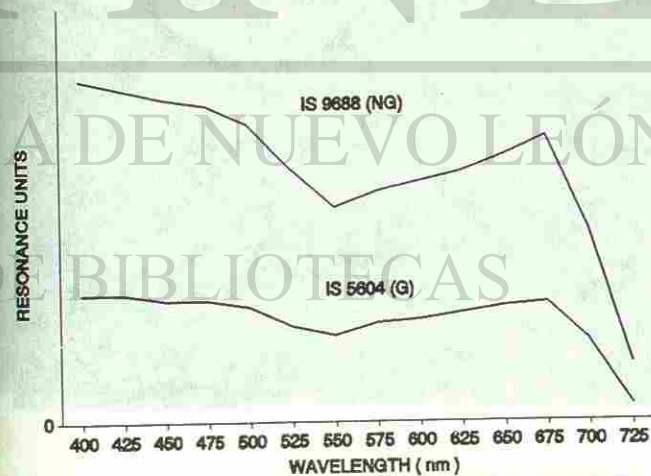


Figure 9.5 Photoacoustic response in glossy (G) and nonglossy (NG) sorghum leaves.

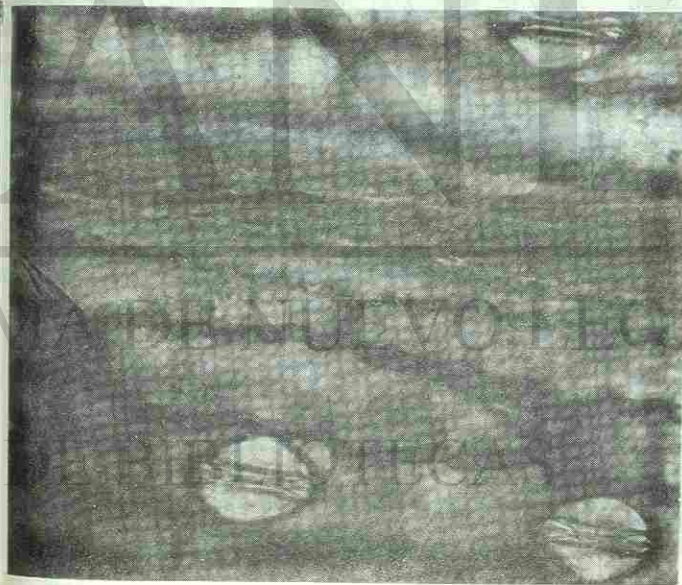
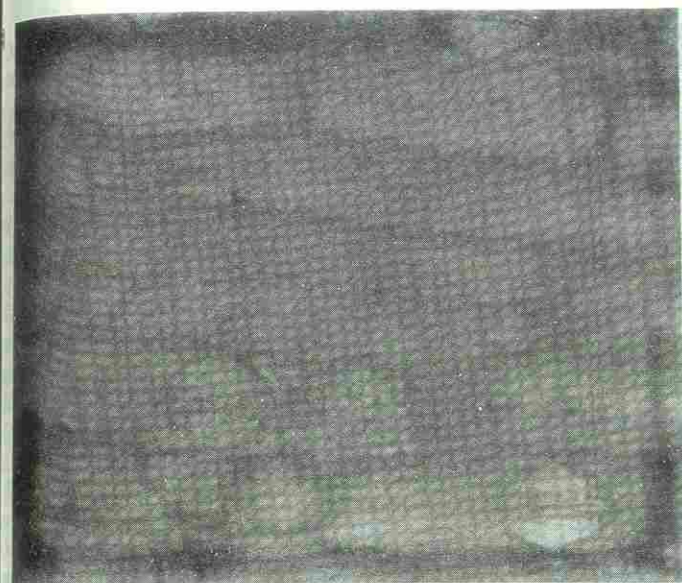
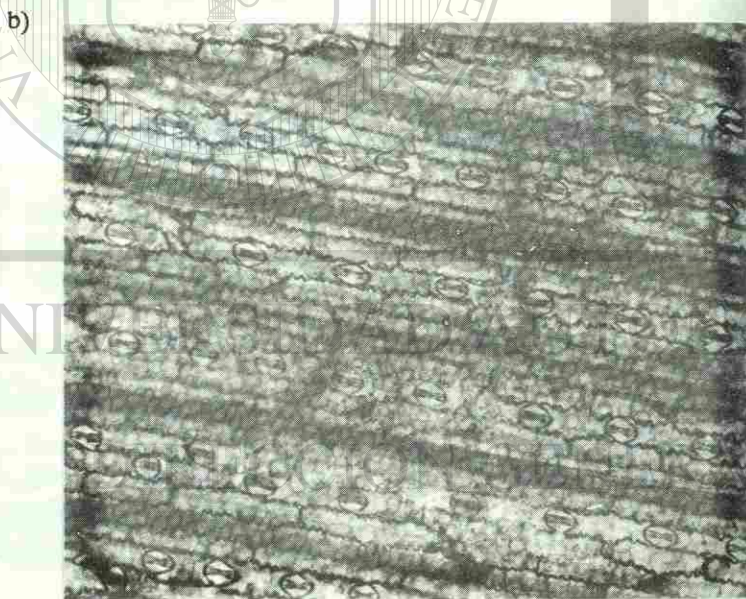
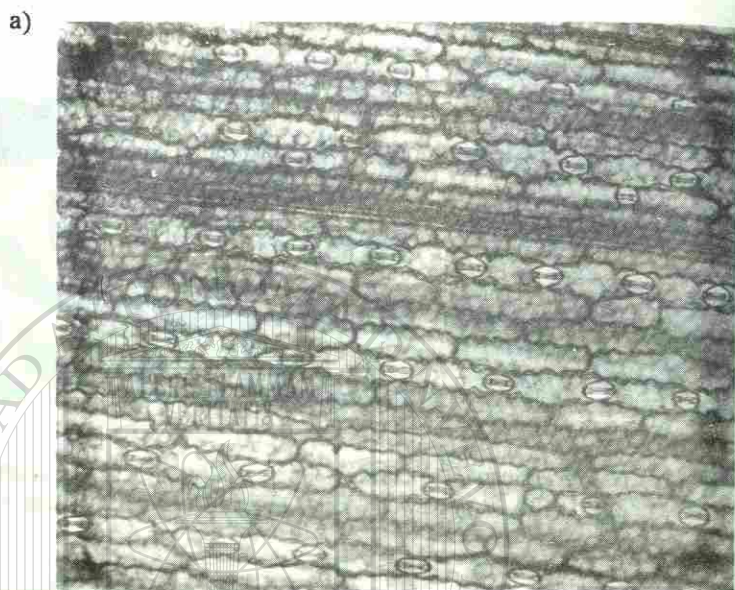


Plate 9.5 Variation in epidermal cell structures in glossy (G) and nonglossy (NG) sorghum genotypes. a) CSH1 (NG) showing general surface morphology and absence of nonglandular trichomes; b) IS 4664 showing general surface

morphology and presence of nonglandular trichomes; c) IS 1062, d) IS 1082 depicting the presence of nonglandular trichomes.

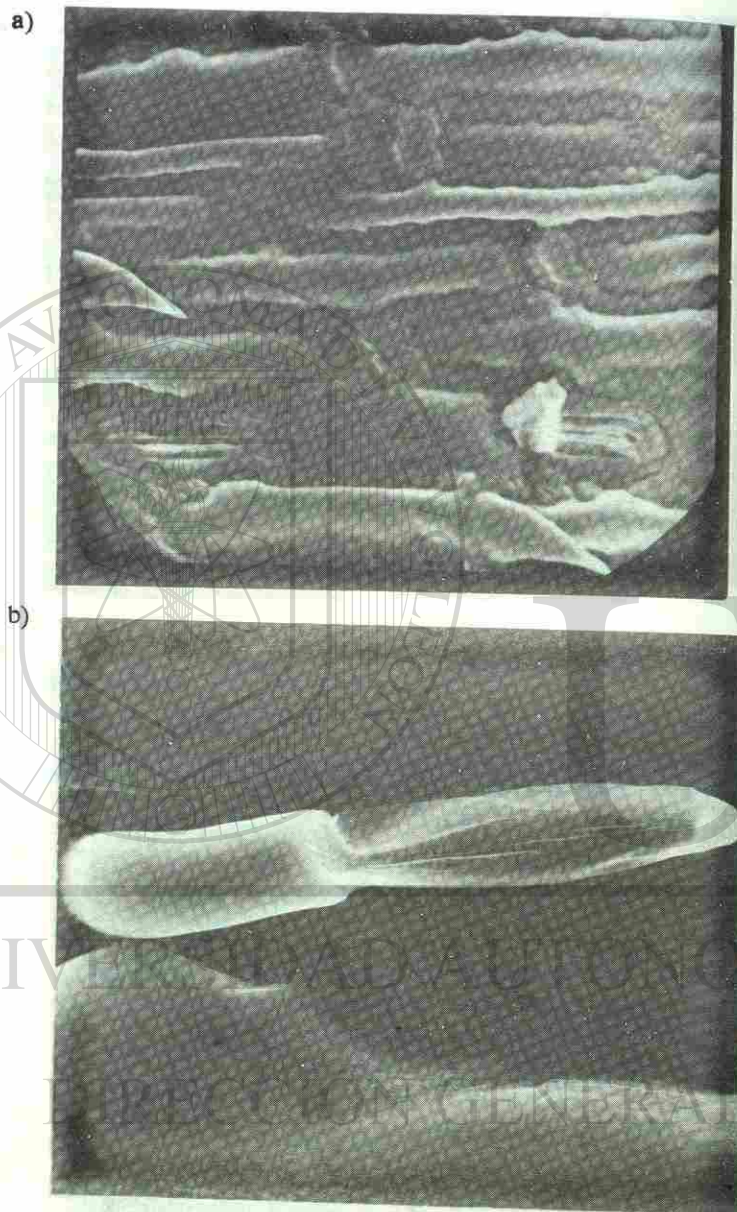


Plate 9.6 Variation in trichome morphology in glossy and nonglossy sorghum genotypes: a) M-35-1 (SEM) showing epidermal cells, stomata, silica crystals and pointed nonglandular trichomes; b) CSH1 showing bicellular trichomes, characteristic of nonglossy sorghum genotypes.

Out of 495 glossy lines, 272 lines had trichomes on both upper and lower surfaces and 169 lines had no trichomes. The leaf surface of only 50 sorghum lines (10 glossy and 10 nonglossy) were studied with scanning electron microscopy (SEM). The glossy lines possessed amorphous smooth waxy lines associated with a smaller number of large irregular crystals in contrast with irregular leaf surface and a large number of needle shaped crystals in the nonglossy lines (Maiti *et al.*, 1984). Nonglossy lines had a high density of needleshaped wax crystals unlike the irregularly shaped crystals reported by Tarumoto *et al.* (1981).

Crop age
Growth analysis indicated that leaf area, plant height and plant dry weight increased with age in both glossy and nonglossy lines. Glossy lines had larger and taller plants with lower leaf area (García-Mendoza, 1986). There was not much difference in epidermal cell, stomata and trichome numbers between glossy and nonglossy lines. Glossy lines had predominantly nonglandular unicellular trichomes and the nonglossy lines bicellular glandular trichomes (Plates 9.5 & 9.6). HCN content in glossy lines showed a slight decrease from seedling up to 45 days but a sharp reduction at 60 days (Fig. 9.6). Nonglossy lines showed a decrease at 30 days with an increase at 45 days and a drastic decrease at 60 days. Wax content increased at 30 days in both glossy and nonglossy lines, but decreased at advanced growth stages. Glossy lines showed higher wax content at 15 days compared to nonglossy ones (Fig. 9.7). Chlorophyll content increased with age in both lines, remaining stable at 45 days in glossy lines, but increasing in nonglossy lines. Chlorophyll content was always higher in nonglossy lines compared to glossy

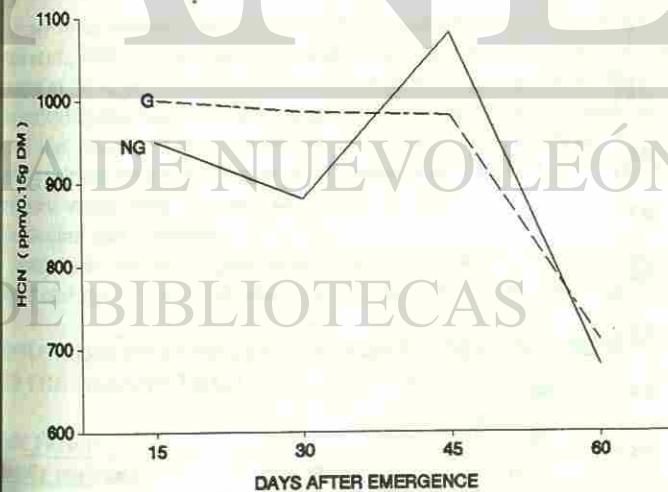


Figure 9.6 Average HCN content (ppm / 0.15 g DM) in glossy (G) and nonglossy (NG) sorghum at different crop age.

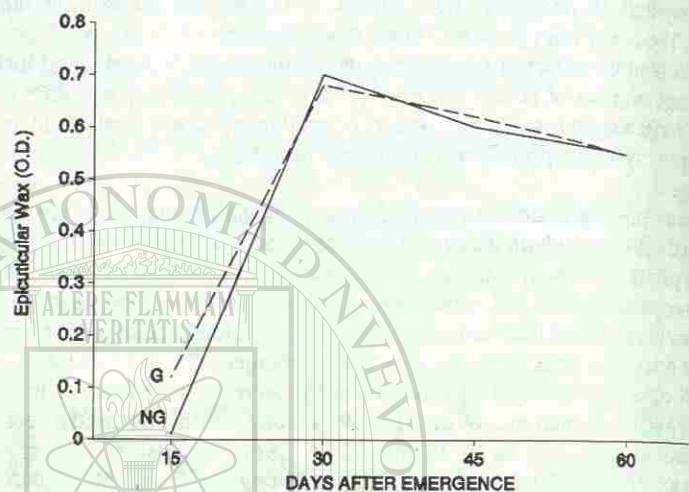


Figure 9.7 Average epicuticular wax content (OD) in glossy (G) and non-glossy (NG) sorghum at different crop ages.

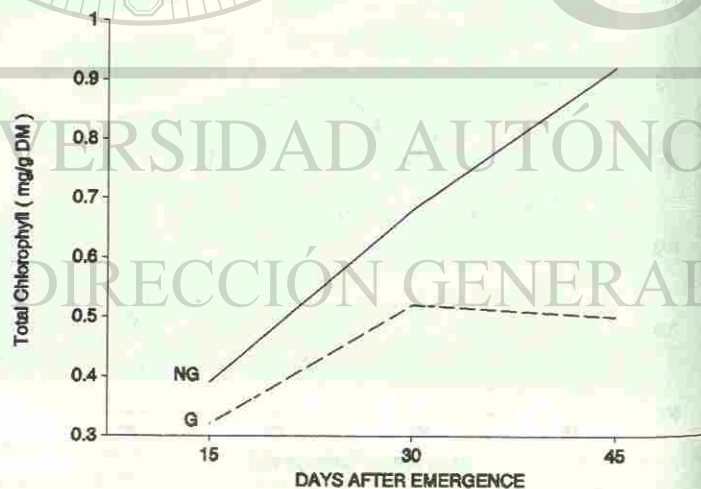


Figure 9.8 Average chlorophyll content (mg/g DM) in glossy (G) and non-glossy (NG) sorghum at different crop ages.

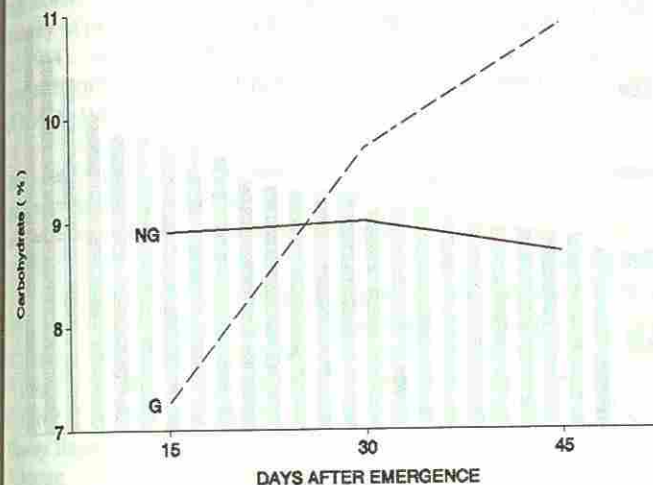


Figure 9.9 Average percentage carbohydrate content in glossy (G) and non-glossy (NG) sorghum at different crop ages.

at all growth stages (Fig. 9.8). Carbohydrate content was higher in nonglossy sorghum at 15 days after emergence, but decreasing at subsequent growth stages, then it showed a sharp increase from 15 to 45 days in glossy ones (Fig. 9.9).

Hydrocyanic acid (HCN)
Glossy lines showed variations in HCN content in the 20-day seedling stage (Sinha *et al.*, 1991). Glossy genotypes showed highly significant differences in HCN contents at 30 days ($F = 23.47$; $P = 0.01$; Fig. 9.10), but not at 45 days ($F = 2.40$). This indicates that variation among genotypes in HCN content decreased with the age of the crop which supports the study of earlier workers. The genotypes showing minimum HCN content at this stage were IS 5622, IS 1054, IS 2205 and maximum value were IS 4661, M-35-585, IS 2312.

Epicuticular wax content

Glossy lines showed highly significant variations in epicuticular wax contents (mg/32 cm² leaf area) at 30-day crop age ($F = 6.15$; $P = 0.01$; Fig. 9.11).

MECHANISMS OF RESISTANCE AGAINST BIOTIC AND ABIOTIC FACTORS AND THE GLOSSY TRAIT

Biotic Factors

Shootfly resistance

Glossy sorghum genotypes (495) and 2 checks, CSH1 and Swarna were evaluated for resistance to shootfly during the post-rainy season, 1981 in India at ICRISAT. Several shootfly incidence indices were recorded.

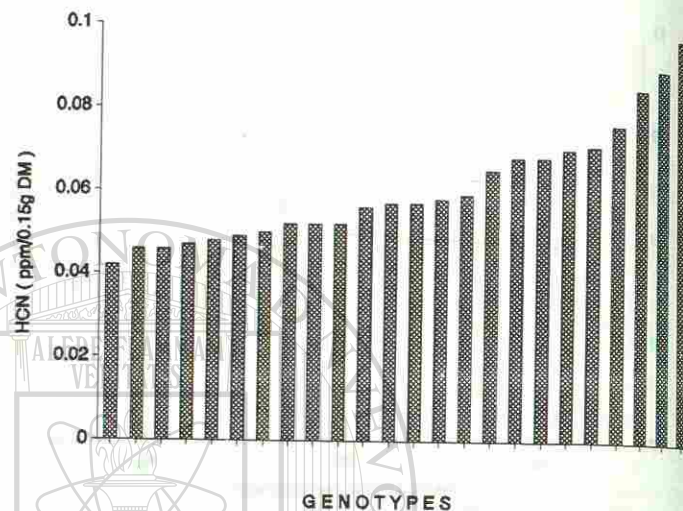


Figure 9.10 Average HCN content in glossy and nonglossy sorghum at 15 days after emergence (ordered according to increasing HCN contents).

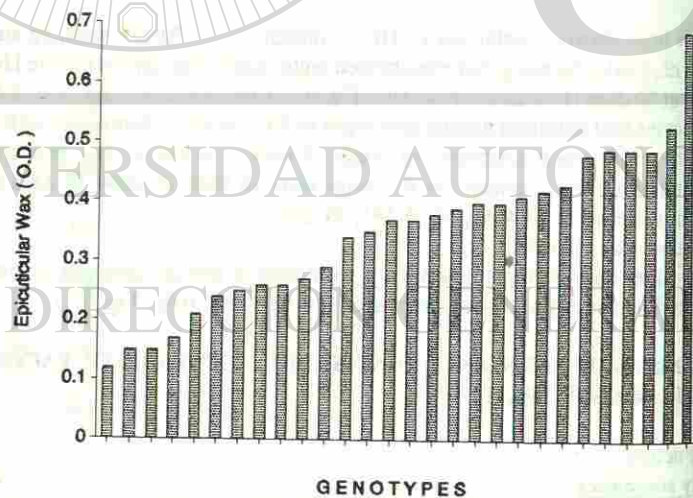


Figure 9.11 Average percentage epicuticular wax (EW) content in sorghum genotypes (ordered according to increasing EW contents).

Glossy lines showed highly significant differences among them for seedling vigor, glossy scores, percent plants with eggs and percent dead hearts (Table 9.6). The variability in percent plants with eggs and deadhearts was also very large (Maiti *et al.*, 1984). All the sorghum lines resistant to shootfly have been found to be glossy, although the levels of resistance vary among them (Maiti, 1980; Agrawal and House, 1982).

Table 9.6 Analysis of variance of seedling vigor, glossy scores and shoot fly incidence parameters (Maiti *et al.*, 1984) (** P < 0.01).

	df	Seedling vigor	Mean square		
			Glossy scores	% plants with eggs	% plants with deadhearts
Rep.	2	0.82 NS	25.56 **	12572.37 **	3095.9 **
Gen.	495	1.73 **	1.04 **	826.54 **	768.34 **
Error	988	0.54	0.26	221.26	174.64
Glossy lines					
Mean		2.6	1.5	45.0	40.2
Range		1.0-4.7	1.0-4.7	12.6-94.7	7.9-90.1
C.V (%)		28.5	32.9	33.0	32.9
Nonglossy lines					
CSH 1		4.0	5.0	80.1	80.8
Swarna		4.0	5.0	74.8	74.8

Mechanism of resistance to shootfly - Trichome presence and density

Many sorghum lines having some field resistance had trichomes on their abaxial surface. In a wider range of materials (germplasm and breeding lines) under varying shootfly pressures, trichomed lines suffer comparatively less (fewer dead hearts) than non trichomed lines (Maiti, 1980; Maiti and Bidinger, 1979; Agrawal and House, 1982; Maiti and Gibson, 1983; Gibson and Maiti, 1983).

The presence of trichomes on the lower surface appears to confer the following advantages: i- reduction in egg laying by the shootfly, and ii- reduction in the deadhearts with the presence of eggs.

Trichomes may be working as a mechanical barrier in the larval movement and causing death of the fly maggots. Therefore, their presence deters oviposition by shootflies. The correlation between trichomes and ovipositional nonpreference is nearly $r=0.8$ (Agrawal and House, 1982). Breeders have been able to reject susceptible at all stages of testing of materials and finally increase the frequency of resistant genes (Agrawal and House, 1982).

Glossy trait

Glossiness is a monogenic recessive trait (Tarumato *et al.*, 1981). A set of genotypes with and without the glossy traits were tested 5 times for shootfly reaction under different fly pressures. Later, cluster analysis was done to categorize them into different groups based on deadhearts incidence. The frequency of glossy

lines in each group was calculated. There was a predominance of glossy lines in the group with the lower mean percentage of deadhearts (Maiti and Bidinger, 1979). With an increase in the level of susceptibility there was an increase in the number of nonglossy lines.

Differences in shootfly damage between glossy and nonglossy as well as trichomed and trichome free genotypes were always significant. At all fly pressures, glossy and trichomed lines overlap in the extent of shootfly damage indicating close association of these traits. Similarly, the differences between nonglossy and trichomefree lines were not significant. The correlations of trichome traits with shootfly indices were rather poor. This shows that the presence of trichomes imparts resistance to shootfly attack, but the increase in the number of trichomes was not seen to increase the level of resistance.

A principal component analysis on contribution of major factors to shootfly resistance, to trichome intensity, glossy intensity, eggs per plant and percentage dead hearts indicate that all traits are closely associated (Omori *et al.*, 1983). Both genotypic and phenotypic correlations made among these variables indicate a high degree of associations among them. Trichome intensity, glossy intensity and dead heart percentage are shown to be highly heritable traits (Agrawal and House, 1982). It is a monogenic recessive trait (Tarumato *et al.*, 1980). Shootfly incidence showed negative correlation with glossy and trichome intensity. These correlations were partitioned to show the contribution of individual trait by path coefficient analysis which indicated that high correlation is the result of exogenous traits and hence the glossy appearance may be an indicator to some other trait that contributes to resistance (Agrawal and House, 1982; Omori *et al.*, 1988). The genotypes showing a greater degree of intensity in glossiness were more resistant to shootfly. They were less affected by both shootfly egg laying and dead hearts (Maiti *et al.*, 1984). Omori *et al.* (1988) reported that trichome density contributed mainly towards genetic divergence in shootfly resistance, followed by glossiness. Heterosis for shootfly resistance was found to be associated with genetic divergence but not with geographic divergence.

There are several factors that contribute shootfly resistance, such as nonpreference for oviposition associated with the presence of trichomes on the leaf surface (Blum, 1968, 1972) and the glossy trait (Maiti and Bidinger, 1979). Similarly, the lignin and silica deposits may contribute towards the mechanical resistance of seedlings to penetration by larvae (Blum, 1968). Low leaf surface wetness (LSW) of the leaf whorl is an important factor in resistance to shootfly (Nwanze *et al.*, 1990). The susceptible lines show high LSW compared to the resistant lines. Glossy lines in general show less LSW depending of course on the intensity of glossiness (unpublished).

Quantitative relationship of morphophysiological traits with shootfly resistance

Some morphophysiological and anatomical traits of shootfly resistant and susceptible lines showed significant difference among them such as trichome number in the upper and lower surface. A correlation analysis has made among parameters determining resistance to shootfly deadheart in a set of lines. The parameters showing significant positive correlation with shootfly resistance (deadhearts) were: high glossy score, high seedling vigor, low leaf surface wetness, less

width and lower stomata number in the upper surface in sorghum genotypes. Trichome number in the upper surface showed significant negative correlation with shootfly deadhearts (unpublished).

Another study with 520 sorghum germplasm determined that intensity of glossiness and trichomes were directly related with shootfly resistance, and not seedling vigor (unpublished).

The distribution of traits for shootfly resistance such as glossy score (GS; 1 to 5 non-glossy), seedling vigor (SV; high or low) and trichomes (T; none, upper leaf surface, upper and lower leaf surfaces) were studied among sorghum genotypes (1992, unpublished). The results indicated that intense glossiness (GS 1-2) persisted in the resistant (against shootfly and deadhearts) and moderately resistant categories, whereas 80 to 95 % of the genotypes of the susceptible classes showed lower glossiness (GS 3-5). This clearly establishes that the intensity of glossiness is positively associated with the level of resistance against shootfly. Similarly, the genotypes with highly vigorous seedlings resulted in plants resistant to shootfly and deadhearts, whereas those genotypes with moderately vigorous seedlings resulted in susceptible or moderately resistant plants. The resistance of the genotypes was also directly related to the presence and density of trichomes. In the resistant classes, the proportion of genotypes with trichomes on both the upper and lower surfaces was greater than in the susceptible classes for oviposition and deadhearts.

A multiple regression equation was computed to determine the effect of the morphophysiological traits on oviposition and damage by shootfly (deadhearts). Up to 40% of the variability could be explained by these traits in the case of oviposition and about 47% in the case of deadhearts. The significant and negative regression coefficients of individual traits indicate that these traits substantially contributed in reducing shootfly damage.

Shootfly infestation was directly related to glossiness intensity score and was lowest in genotypes with high glossy score. Similarly, shootfly infestation increased in less vigorous genotypes and the lowest shootfly infestation was recorded when trichomes were present on both leaf surfaces followed by the presence of trichomes only on the upper surface. The highest infestation was recorded in the genotypes when the trichomes were absent on both leaf surfaces. Therefore, the presence of high glossy intensity and of trichomes on both surfaces of the leaf can be considered as reliable selection criteria in breeding for shootfly resistance.

Glossy characteristics and its role in genetic improvement in shootfly resistance

About 493 sorghum lines with varying glossy intensity were selected for their possible utilization in breeding for shootfly resistance. These genotypes were distributed in groups depending on their resistance (shootfly oviposition and deadhearts) and their characteristics of glossy intensity (GS 1-5), geographical origin and taxonomic group. None of the genotypes was highly resistant (< 10% infestation) to shootfly for any of the resistance parameters. The genotypes in the resistant and moderately resistant categories (which made up 63-73% of the genotypes) had GS 1 or 2, with just a few having GS 3-5 in the moderately resistant group. Almost all of the genotypes with GS from 3-5 belonged to the susceptible group (27-37% of the genotypes). Shootfly infestation increased as the

glossy intensity decreased. Genotypes with glossy score 1 had 40% oviposition and 35% deadhearts as against 74% oviposition and 69% deadhearts with glossy score 5. This establishes that the intensity of glossiness is positively associated with the level of shootfly resistance.

Of the Indian genotypes (83% of the genotypes), the majority were moderately resistant (47%) to shootfly, and moderately resistant to deadhearts (49%). Of the Indian genotypes, 24-36% were susceptible to shootflies and to deadheart damage. Half of the genotypes of African origin (12% of the genotypes) were susceptible for oviposition and deadhearts. Greater proportions of the genotypes of USA origin (5% of the genotypes) were either in the resistant or moderately resistant groups. The majority of genotypes with Indian and USA origin may be sources of higher resistance levels. The basis for the evolution of shootfly resistance is understandable, because shootfly has been a pest of sorghum in India since immemorial times. However, the sorghums genotypes of USA origin might not have exposed to insect infestations, since shootfly is absent in USA.

Considering glossy score, geographic origin and taxonomic race, minimum shootfly infestation was recorded in genotypes of USA origin and Bicolor race in glossy score 1. However in glossy score 2, Durra sorghums with Indian origin had the minimum shootfly infestation (Table 9.7). Maximum infestation was observed in Guinea sorghums of Africa, even with high glossy intensity, though the number of genotypes in this category were few (5). The variance ratio between genotypes and environment for shootfly resistant parameters viz. oviposition deadhearts among the glossy scores are shown in Table 9.7. The genotypes were significantly different for shootfly resistance parameters within each glossy score. Furthermore, genotype variation was higher for deadhearts compared to oviposition among the lines with high glossy intensity.

Table 9.7 Ratios of genotype to error mean squares (F ratio) for shootfly resistance parameters in different glossy score classes (** P=0.01; * P=0.05).

Glossy score	Resistance parameters	Geographic origin			Taxonomic races		
		Africa	India	USA	Bicolor	Caudatum	Durra
1	Oviposition	8.71**	3.26**	3.17**	3.56**	2.84	3.66**
	Deadhearts	9.54**	3.36**	5.32**	4.97**	3.36*	3.77**
2	Oviposition	2.48**	2.23**	-	1.41	5.84**	2.35**
	Deadhearts	3.56**	2.62**	-	2.29	8.34**	2.76**
3&4	Oviposition	1.57	2.76*	-	-	-	3.56*
	Deadhearts	2.05	3.66**	-	-	-	5.50**
5	Oviposition	-	2.84*	-	-	-	2.23
	Deadhearts	-	2.11	-	-	-	2.48

Correlation studies between oviposition and deadhearts in different geographic origin, taxonomic races and glossy scores showed that in all cases the coefficients were highly significant indicating close relationships between these shootfly resistance parameters (Table 9.8). Only in one case, no significant correlation was

observed between oviposition and deadhearts in genotypes of African origin with glossy scores 3-4.

Table 9.8 Correlations between oviposition and deadhearts in different geographic origin, taxonomic races and glossy scores (** P=0.01).

Glossy score	Geographic origin			Taxonomic race		
	Africa	India	USA	Bicolor	Caudatum	Durra
1	0.95**	0.85**	0.88**	0.85**	0.96**	0.86**
2	0.91**	0.84**	-	0.83**	0.96**	0.85**
3&4	0.71	0.91**	-	-	-	0.90**
5	-	0.93**	-	-	-	0.84**

In order to assess the advantage of glossy trait for breeding of shootfly resistance, heritability percentage was calculated under geographical and taxonomic classification of glossy scores. Among the geographical groups, the heritability (%) was positively related with the level of glossiness in the genotypes both of Indian and African origins. Glossy characteristics play an important role in improving the heritability component in shootfly resistance parameters. This suggests that genotypes of African origin with high glossy score are better for breeding programs improving shootfly resistance. Similar trends between glossiness and shootfly resistance parameters were observed for taxonomic groups. High glossiness contributes favorably for heritability improvement for both the resistance parameters in Caudatum and Bicolor races compared to Durra. But this needs further confirmation with a larger number of genotypes of the Caudatum and Bicolor races. Glossy Durra sorghum of African origin can contribute well in the breeding program for shootfly resistance.

Epicuticular wax (EW) structure (scanning electron microscopy, SEM) in relation to shootfly resistance

Sorghum genotypes with waxy bloom are reported to be drought and insect resistant (Blum, 1975b; Chaterton *et al.*, 1975), improving their productivity in arid and semiarid climates by reducing transpiration and increasing water use efficiency. Wax filaments types reported in *Sorghum bicolor* include tubular (Sánchez-Barral *et al.*, 1972), and filament- and ribbonlike (Atkins and Hamilton, 1982). p-Hydroxybenzaldehyde, a chemical contained in the EW of sorghum seedling leaves is considered as major factor in reducing locust feeding, and related to the resistance to stem borer (Woodhead and Taneja, 1987). EW causes disorientation of stem borer larval movement (Taneja and Woodhead, 1989). Waxes with correct physical characteristics and chemical composition are effective against insects. Sticky waxes may stick the insect claws and feet to the leaf surface thus providing grip necessary to the insect to move around effectively (Atkin and Hamilton, 1982; Mauseth, 1988).

It was mentioned earlier that glossy genotypes vary widely in epicuticular wax structure. The smooth epicuticular waxy surface associated with trichome density

probably offers resistance to shootfly oviposition and maggot movement on the slippery leaf surface which needs to be confirmed in future study. Genotypes IS 2205, IS 2312, 2396, IS 4776, IS 5282 and 5359 showed the same characteristics and were found to show high level of shootfly resistance (Sharma *et al.*, 1992). In this study IS 5282, IS 3962, IS 4576 and IS 2205 also showed high field resistance in oviposition nonpreference and deadhearts percentage.

Correlation studies between plant height and numbers of days to 50% flowering with shootfly resistance

Sorghum lines (525) varying in the intensity of leaf surface glossiness at the seedling stage have been used to study the relationship of plant height and days to flower with shootfly incidences. The data on shootfly resistance parameters viz. % plants with shootfly eggs (PE %) and % plants with deadhearts (PD %) and plant height (PH) and days to flowering (DF) were taken from Entomology and the Genetic Resources Unit, ICRISAT. The correlations among plant characters and shootfly resistance parameters are given in Tables 9.9 & 9.10.

Table 9.9 Correlations among morphological and shootfly resistance parameters in glossy lines.

Characters	DF	PH	PE %
PH	0.110 *		
PE %	-0.200 **	0.003	
PD %	-0.227 **	-0.067 *	0.885 **

[PH : Plant height; DF = Days to 50 % flowering; PE % = Percent of plants with shootfly eggs; PD % = Percent of plants with deadhearts. *, ** Significant at 5% and 1% level respectively.]

Table 9.10 Correlations among morphological and shootfly resistance parameters in nonglossy lines.

Characters	DF	PH	PE %
PH	0.106		
PE %	-0.278	0.062	
PD %	-0.178	0.058	0.886**

[PH : Plant height; DF = Days to 50 % flowering; PE % = Percent of plants with shootfly eggs; PD % = Percent of plants with deadhearts. ** Significant at 1% level.]

Days to flowering had negative and significant association with percent plants with eggs and percent plants with deadhearts among glossy lines. Nonglossy lines showed a similar but nonsignificant association. This indicates that high glossiness and intensity and late flowering are advantageous in decreasing shootfly susceptibility. The relationship between plant height and shootfly resistance parameters (PE % & PD %) were found negligible in both glossy and nonglossy groups.

Regression equations have been fitted among glossy and nonglossy genotypes in order to estimate the extent of the effects of plant height and days to flowering

shootfly incidence (Table 9.11). Days to flowering had significant effect on shootfly incidence, whereas plant height and days to flower and their interaction contributed substantially on shootfly damage among glossy genotypes. The relationship among these traits was negatively linear for nonglossy genotypes. Plant height played an important role both on egg nonpreference and shootfly damage. Days to flower and plant height showed a positive linear relation with percent damage. Plant height and days to flower were directly related to shootfly parameters among glossy genotypes.

Table 9.11 Response coefficients of plant height (PH) and days to flowering (DF) in different functions (* P=0.05, ** P=0.01).

Functions	PH	DF	(PH X DF)
Glossy lines			
PE % / (PH, DF)	0.010	-0.342 **	
PD % / (PH, DF, PH X DF)	-0.177	-0.868 **	0.002
PD% / (PH, DF)	-0.016	-0.360 **	
PD% / (PH, DF, (PH X DF))	-0.303 **	-1.169 **	0.004 **
Nonglossy lines			
PE% / (PH, DF)	0.025	-0.401	
PE% / (PH, DF, PH X DF)	0.809 *	1.630	-0.011 *
PD% / (PH, DF)	0.022	-0.273	
PD% / (PH, DF, PH X DF)	0.908 **	2.024 *	-0.001 **

Table 9.12 Test of independence between shootfly resistant levels, plant height and days to flowering among glossy lines (* P=0.05, ** P=0.01).

Comparison	df	X ²
Plant height vs % PE	4	4.59
Plant height vs %PD	4	9.74 *
Days to flower vs %PE	4	22.82 **
Days to flower vs % PD	4	30.18 **

An interdependence between shootfly resistance levels, plant height and days to flower among glossy lines has been tested using X² statistics (Table 9.12). Ovipositional preference (PE%) was independent of plant height, whereas shootfly damage was found significantly dependent on plant height. Similarly, PE% and PD % were highly dependent on days to flowering to shootfly resistance among glossy lines. These characters are further grouped into 3 plant height classes, i.e., dwarf (less than 150 cm), medium (150-250) and tall (more than 250 cm) and 3 flowering groups, early flowering (less than 70 days), intermediate (70-90 days) and late (more than 90 days). It was confirmed that days to flowering played an

important role on oviposition preference, but not plant height. Tall and late flowering genotypes seem favourable in reducing shootfly incidence.

Other insects and diseases

It has been recently reported that 50% of shootfly resistant lines having glossy trait are resistant to stem borer (Nwanze *et al.*, 1991). Scientist from the Centre for Overseas Pest Research, London while working at ICRISAT had some indications that glossy lines which were tolerant to shootfly were also tolerant to flea beetle (*Perigrinus* sp.) and shoot bug (*Perigrinus maidis*) (Susan Woodhead, COPR, U.K., personal communication). Tarumoto from Japan (personal communication, 1981) stated that the glossy lines were resistant to sorghum leaf blight caused by *Exserohilum turcicum*.

ABIOTIC STRESSES

Seedling drought resistance

Significant genotype differences among sorghum genotypes in response to drought were found. During the process of standardization of testing for seedling drought, it was noticed that most seedling drought resistant lines were glossy and recovered faster after the release of stress in field conditions (Maiti *et al.*, 1984).

Glossy and nonglossy lines were analyzed separately and analysis of variance revealed that glossy lines did not show much divergence in drought resistance. But significant differences were observed among nonglossy lines. The t-test between glossy and nonglossy lines also showed significant differences in various drought resistance parameters. Under stress, the growth rate was checked in nonglossy lines compared to glossy ones (Maiti, 1986). Nonglossy lines at early seedling stage were more vigorous than glossy lines. The glossy lines showed more resistance than nonglossy lines. Cluster analysis showed that about 87% of the resistant lines which fell in cluster 1 were glossy ones while all of the susceptible lines which formed cluster 4 were nonglossy (unpublished).

Glossy lines showed statistically significant differences from the nonglossy in several drought resistance parameters, e.g. visual score for wilting, recovery score, and percent survival of seedlings (unpublished).

Glossy lines showed higher water use efficiency in terms of water required to produce one gram of dry weight compared to the nonglossy lines in solution culture studies (Sullivan and Maiti, 1983, unpublished). In carbowax induced water stress, glossy lines were more tolerant to water stress compared to the nonglossy lines. The reduced transpiration and high water efficiency might be an adaptation of glossy lines for drought (Table 9.13). Glossy lines in general had higher water use efficiency (WUE, glossy - WUE = 12.65, Nonglossy - WUE = 9.66, avg.), but few glossy lines had low WUE and few nonglossy had also high WUE.

With respect to shoot/root ratio there was no clearcut distinction between glossy and nonglossy lines, some glossy lines had low values indicating higher root growth compared to shoot growth. This was also true in case of some nonglossy lines.

Experiments were conducted in a green house at ICRISAT to study the comparative efficiency of glossy lines over nonglossy both under water stressed and unstressed situation (June-July 1992).

The mean values of some morphophysiological characters are shown in Table

9.13. Glossy lines showed superiority in growth (shoot, root and shoot + root dry weight) over nonglossy lines under water stress and control condition. F-ratio for glossy vs nonglossy indicate highly significant differences for root and shoot growth (dry weight) under water stress, but the differences were found significant only in case of shoot growth under control. The difference between glossy and nonglossy lines was higher under water stress compared to unstressed conditions.

Table 9.13 Water use efficiency (WUE) of glossy and nonglossy sorghums at Agronomy Faculty, University of Nebraska (Sullivan & Maiti- unpublished).

Genotypes	WUE \$	Dry weight, g		Shoot/ root
		Shoot	Root	
IS 2394 (G)	14.6	8.4	2.0	4.2
RS 671 (NG)	12.1	21.6	5.0	4.4
IS 2962 (G)	17.3	15.1	3.5	4.2
CSV5 (NG)	11.4	11.6	3.4	3.4
IS 4449 (NG)	9.9	11.4	3.5	3.3
IS 15701 (NG)	10.0	11.6	4.6	2.5
IS 4405 (G)	9.0	16.4	4.4	3.7
IS 6205 (NG)	8.9	14.8	5.3	2.8
IS 9040 (NG)	6.4	11.1	7.0	1.7
IS 226 (NG)	9.0	18.9	7.6	2.5
IS 5567 (G)	13.9	14.6	4.8	3.1
IS 4621 (G)	9.7	20.7	7.3	2.8
IS 1096 (G)	11.4	15.1	5.3	3.0
IS 15701 (NG)	9.6	21.8	8.5	2.6

Plants were grown hydroponically in plastic cylinders (15.4 X 7.7 cm). The plants were harvested at 72 days after germination.

Table 9.14 Mean values of some morphophysiological characters of glossy and nonglossy groups of sorghums (SDW = Shoot dry weight, g; RDW = Root dry weight, g).

Variable	Mean values			
	Water		Stress	
	Glossy	Nonglossy	Glossy	Nonglossy
SDW	1.123	0.938	0.269	0.124
RDW	0.404	0.397	0.078	0.052
Total	1.527	1.335	0.347	0.177

The ratio of glossy to nonglossy again revealed the superiority of glossy over nonglossy under stress condition for root and shoot growth but under unstressed

situation the values of the ratios were less compared to stress condition (Table 9.15).

Table 9.15 Water use efficiency (root growth - RT and shoot growth - SH) of glossy and non-glossy group under water stress and unstressed condition.

Group	Control (10^{-4})			Stress (10^{-4})		
	RT	SH	R+S	RT	SH	R+S
Glossy	10.03	27.90	37.93	1.40	4.75	6.15
Non-glossy	9.98	23.50	33.50	0.95	2.20	3.12
GL/NGL	1.01	1.19	1.13	1.47	2.14	1.97

Glossy genotypes showed superiority over nonglossy ones for shoot, root and total dry weight under both water and unstressed condition (Table 9.16). F-ratios in the analysis of variance reveal that the genotypic variation among the glossy genotypes was highly significant for all characters under water and stress conditions. Although the variations among nonglossy lines were significant for these characters under water treatment, no variation was found under stress conditions. This means that under stress, glossy genotypes have advantage over nonglossy for genetic improvement of drought resistance. This was further confirmed from the heritability estimates for glossy genotypes under water and stress conditions (Table 9.17).

Table 9.16 Mean values (dry wt, g) and ANOVA of some morpho-physiological characters under water and stress condition.

SV	Water treatment			Stress		
	F-values			F-values		
	Shoot	Root	Total	Shoot	Root	Total
GL/NGL	16.20**	16.29**	4.17*	5.47*	0.53	3.25
GL	3.54**	6.71**	3.86**	3.48**	3.90**	3.72**
NGL	3.40**	2.17*	3.27*	0.54	0.12	0.32
Mean						
Glossy	2.51	0.50	3.02	0.22	0.056	0.28
Non-glossy	2.27	0.59	2.87	0.19	0.049	0.24

Effect of water stress on some physiological and biochemical components

García-Saucedo (1985) made a study of the effect of water stress on root growth, leaf area, transpiration and biochemical components like HCN, chlorophyll and carbohydrates of some glossy and nonglossy lines. HCN content in leaves increased considerably under drought stress with the decrease in optimum mois-

Table 9.17 Heritability of shoot, root and total dry weight under stress and non-stress situation (W = Water, S = Stress).

		Shoot dry weight	Root dry weight	Total
Glossy:	(W)	13	26	34
	(S)	36	95	79
N.Glossy:	(W)	12	6	27
	(S)	0	0	0

level. There existed variation in HCN content among glossy and nonglossy under water stress which is a character related to drought tolerance. Carbohydrate content increased from optimum to moderate water stress level in both types, but decreased at higher water stress. At the same time, chlorophyll content decreased thus affecting the photosynthetic activity. However, some lines showed significant decrease under water stress. The rate of transpiration decreased with increase in epicuticular wax content (Tables 9.18 and 9.19).

Table 9.18 Variability in HCN content, chlorophyll and carbohydrate at 3 levels of moisture.

Genotypes	HCN mg			Chlorophyll mg dry wt.			Carbohydrates mg dry wt.		
	a1	a2	a3	a1	a2	a3	a1	a2	a3
IS 18390 (G)	17.0	17.5	34.5	1.6	0.96	-	1260	3213	2760
IS 183590 (G)	16.5	11.8	17.7	1.2	1.13	1.05	1101	3079	2888
LES-2R (NG)	18.0	12.2	17.7	1.0	0.55	-	1328	3214	2862
LES-10R (NG)	19.0	25.7	31.0	1.06	1.06	1.09	1188	2647	2832

Water levels: a1 = each 7 days; a2 = each 15 days; a3 = each 30 days.

Table 9.19 Rate of transpiration (every 2 days) in glossy and nonglossy sorghum (g H₂O).

Genotypes	5 Dec.	7 Dec.	9 Dec.	12 Dec.	14 Dec.	%
IS 18390 (GL)	1.8	4.2	7.4	11.4	16.6	16.5
IS 18590 (GL)	3.1	7.7	13.7	23.5	36.4	30.9
LES-2R (NGL)	2.5	6.0	10.6	17.1	25.6	30.9
LES-10R (NGL)	2.3	5.6	10.1	16.7	24.8	25.1

Variability in intensity of glossiness and waxiness and its relation with water stress resistance

Ríos-Leal (1990) showed that the intensity in glossiness and waxy bloom contribute to higher water stress resistance compared to those having lower intensities. The epidermal cell, stomata and trichome number increased under water stress in all genotypes, although in some lines with higher intensity of glossiness and waxy bloom, epidermal cell and stomata number were more stable. Carbohydrate and HCN content increased under water stress, but the proportion was higher in genotypes having higher intensity of glossiness and waxy bloom compared to ones having lower intensity. The genotypes having higher glossiness showed higher epicuticular wax and also had less loss of water by transpiration (Figs. 9.12 - 9.15).

Mechanism of drought resistance in glossy lines

Glossy lines differ from nonglossy ones in the structure of their epicuticular wax. Under SEM, glossy leaves have smooth wax with large crystals, whereas nonglossy leaves show absence of smooth wax and presence of small needle shaped crystals. The glossy lines during seedling stage showed higher water use efficiency and less water loss by transpiration (Maiti, 1986). Besides some biochemical characters like chlorophyll, carbohydrate, wax and HCN content were reported to be associated with drought resistance (García-Saucedo, 1986; Ríos-Leal, 1990). Rodríguez-Cabrera (1987) showed that glossy lines had better growth under decreasing sprinkler irrigation compared to nonglossy lines.

The EW on sorghum leaf blades imparts drought resistance and therefore, the screening of sorghum genotypes for increased wax may have direct impact for

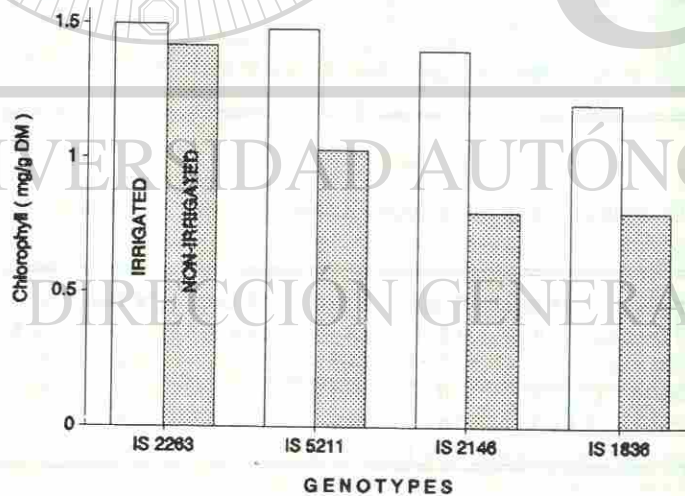


Figure 9.12 Total chlorophyll content (mg/g DM) in 4 glossy lines under irrigated and drought conditions in growth chamber.

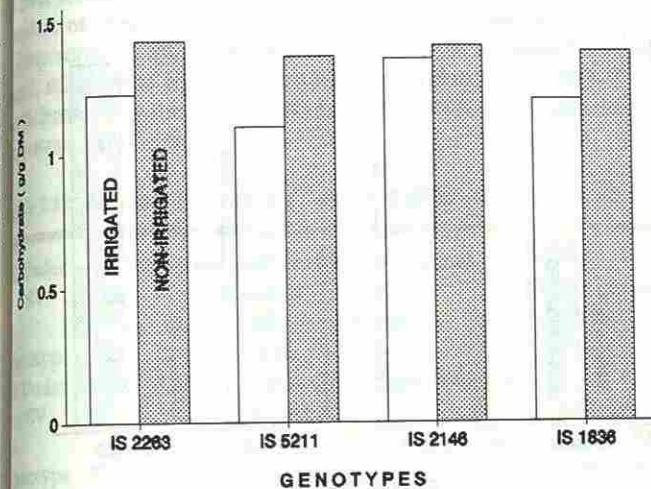


Figure 9.13 Carbohydrate content (g/g DM) in 4 glossy lines under irrigated and drought water stress situations.

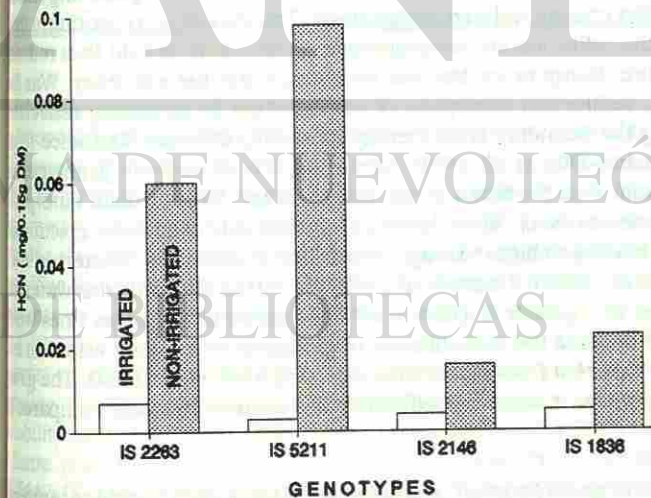
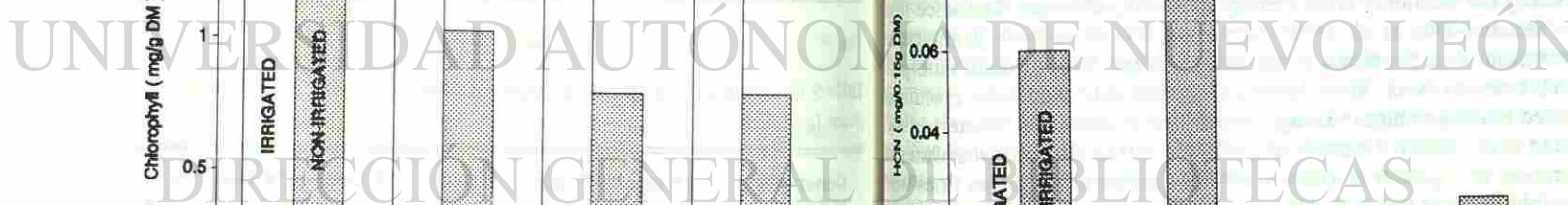
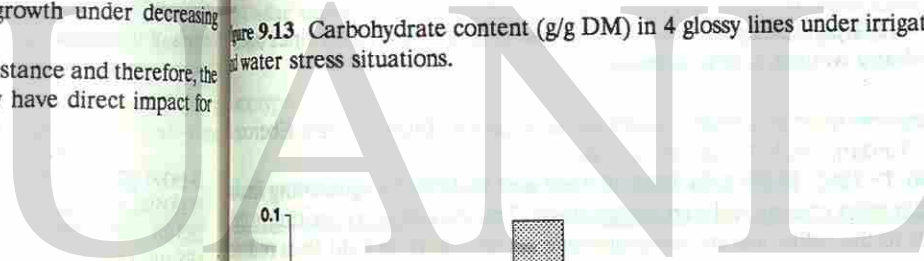
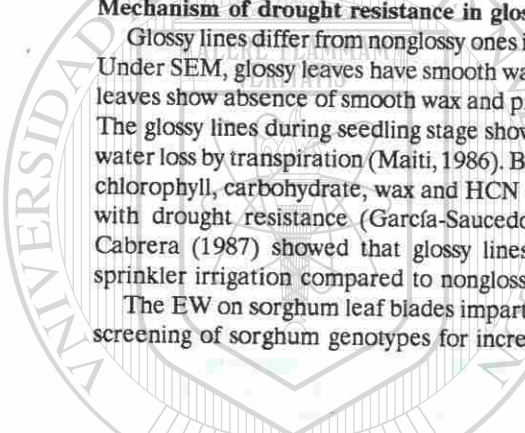


Figure 9.14 HCN content (mg/0.15 g DM) in four glossy lines under irrigated and drought water stress situation in growth chamber.



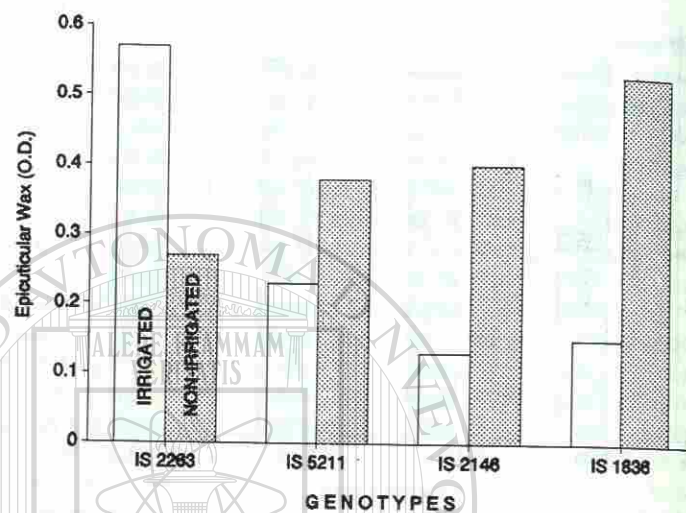


Figure 9.15 Epicuticular wax content and transpiration in 4 glossy lines under irrigated and water stress situations.

genetic improvement of drought resistance in sorghum (Blum, 1975b; Ebercon *et al.*, 1973; Jordan, 1983; Jordan *et al.*, 1984).

IS 1096, IS 2205, IS 2312, IS 5282, IS 5567 and IS 4776 had glistening smooth epicuticular waxy coating and were highly glossy. The smooth waxy coating in these lines leads to the reflection and transmittance of the radiation load thus reducing leaf temperature, transpiration loss and increased water use efficiency. Wax filaments seem to reduce the absorption of net radiation by increasing reflectance and thickening the boundary layer thereby increasing diffusive resistance to gas exchange (Sánchez-Días *et al.*, 1972). In normal, bloom sorghum genotypes has more epicuticular wax deposited in the lamina in the form of thick amorphous layers with filaments of wax (Blum, 1975b). Under drought conditions, epicuticular wax increased leading to higher drought capability of genotypes (Chaterton *et al.*, 1975; Jordan *et al.*, 1984). Traore *et al.* (1984) reported that cuticular water loss by transpiration was greater in glossy leaves compared to nonglossy lines which is questionable because the identification of glossiness by spraying water on leaf surface is quite different from the technique used by Maiti *et al.* (1984). The glossy lines have shown higher water use efficiency and drought recovery compared to nonglossy lines.

Temperature

The response of glossy (tropical) and nonglossy (temperate) to varying temperatures at the seedling stage was studied. Glossy sorghum showed higher levels of tolerance to higher temperatures compared to temperate ones (nonglossy) at the seedling stage, while the temperate sorghum showed tolerance to lower tempera-

Again, glossy sorghum showed a wide range of adaptability in both higher and lower temperatures (López-Irisson, 1990).

Selection of glossy sorghum for different stress resistance

Glossy sorghum genotypes seedlings (28) were evaluated for resistance to drought, salinity and high temperature (García-Sandoval, 1991). The genotypes were different for some of the resistance traits related to drought, salinity and high temperature (Tables 9.20).

Table 9.20 Analysis of variance (F-ratio) of different morphological variables.

Under seedling stress and no-stress situation:

SV	df	Control			Water stress		
		RL	SDW	RDW	RL	SDW	RDW
Genotype	27	2.16 *	4.86 **	1.74	0.97	2.97 **	1.64

Under saline (0.2M) and no-saline stress situation:

SV	df	Control				Salinity			
		SH	RL	SDW	RDW	SH	RT	SDW	RW
Genotype	27	6.65	3.91	7.61	7.78	11.44	3.04	9.52	6.31
Error	56	**	**	**	**	**	**	**	**

Under moderately high (35°C) and optimum (28°C) temperatures:

SV	df	Control				High Temperature			
		SH	RL	SDW	RDW	SH	RT	SDW	RW
Genotype	27	9.56	4.51	6.45	5.77	5.0	2.51	12.5	6.7
Error	56	**	**	**	**	**	**	**	**

RL = Root length, cm; SDW = Shoot dry weight, g; RDW = Root dry weight; * P=0.05, ** P=0.01

Tolerance indices for different stress resistances were calculated by adopting the following formula: Tolerance index (TI) = {Dry weight of seedling under stress / Dry weight of seedling under control}. TI values under stress are given in Table 9.21. The glossy sorghum genotypes (28) showed a wide range of TI under different stresses. TI of the root were much higher than those of the shoot. This indicates that the root maintained higher growth as a method of osmotic adjustment. The following genotypes showed high indices of tolerance for drought and resistance to salinity at the seedling stage: IS 5359, IS 5692, IS 3962, IS 1034, IS 2312, IS 4473, IS 5282, IS 8977, IS 5484, IS 2205, IS 4576, IS 5604. The majority of the glossy lines were well adapted to different stress conditions, including drought, salinity and high temperature. Of course, there exists large variability among glossy genotypes in their response to different stress conditions. Some genotypes were selected for multiple resistance for all these stresses (IS 5642, IS 1096, IS 5692, IS 5359 and IS 4545). HCN content showed an increase in those genotypes subjected to multiple stress, except for IS 1096 which showed constant levels (García-Sandoval, 1991). This could be related to a mechanism of stress resistance.

Table 9.21 Tolerance indices (TI) of 28 glossy sorghum genotypes under different stress conditions.

Genotypes	Water stress		Salinity		High temp. °C	
	TIS	TIR	TIS	TIR	TIS	TIR
IS 5359	2.25	5.27	1.14	1.56	2.89	3.56
IS 5692	1.67	0.88	0.64	1.38	2.44	3.77
IS 3962	1.32	0.40	0.94	1.81	2.73	4.02
IS 1034	1.56	2.44	0.77	1.21	2.62	6.19
IS 8315	1.16	0.96	1.04	1.57	3.39	6.05
IS 2312	1.09	0.86	0.94	0.88	2.42	4.76
IS 4473	1.07	1.49	0.90	0.89	2.25	5.02
IS 5282	1.06	1.17	0.85	1.18	2.92	5.46
IS 8977	0.98	1.33	0.86	1.04	2.78	6.12
IS 5484	0.93	1.11	0.80	1.13	2.54	6.97
IS 2205	0.90	1.57	0.89	1.18	2.72	6.82
IS 4576	0.89	1.10	1.00	1.57	2.01	3.88
IS 5604	0.89	1.36	1.00	1.47	2.84	7.37
IS 4545	0.88	0.66	0.64	1.06	4.58	10.28
IS 8311	0.86	0.74	0.93	1.32	2.05	2.86
IS 5642	0.85	1.11	1.28	1.37	2.62	5.20
IS 4776	0.80	1.32	0.96	1.16	2.46	6.08
IS 5622	0.79	0.84	1.01	1.51	2.97	6.35
IS 18390	0.77	0.71	0.99	1.11	2.50	6.08
IS 4661	0.77	0.89	0.93	1.38	2.01	4.95
IS 4663	0.75	0.78	0.71	0.86	3.23	5.53
IS 5587	0.75	1.06	0.91	1.25	2.23	4.26
IS 1054	0.72	1.00	0.93	1.11	2.07	4.40
IS 2396	0.70	0.65	1.10	1.72	2.10	3.66
IS 1096	0.69	0.96	0.79	1.13	3.52	7.92
IS 5567	0.65	0.86	0.85	1.17	2.18	5.46
IS 4405	0.64	0.90	1.05	1.29	2.23	3.85
IS 2146	0.58	0.93	0.92	1.22	2.07	4.03

NUTRIENT DEFICIENCY**Phosphorus uptake**

Study on phosphorus uptake by glossy and nonglossy lines has shown that glossy lines were more efficient in phosphorus uptake under low phosphorus compared to nonglossy ones (Raju *et al.*, 1987.).

Uptake of minerals

A set of glossy lines have been evaluated for uptake of macro and micro elements under no stress and water stress situation at the seedlings stage (Table 9.22). The results show that the genotypes showed highly significant differences in the uptake of Fe, Zn, Na, Ca and Mg under irrigated condition, but for Fe and

under drought situation. Some genotypes were selected for efficient uptake of minerals under both the situations.

Table 9.22 Analysis of variance for uptake of nutrients under irrigated and seedling drought conditions [** P=0.01].

A) Uptake of nutrients under irrigated conditions (F-ratios):

SV	df	Fe	Zn	Na	Ca	Mg
Genotype	27	4.67	3.72	3.54	6.18	3.42
Error	56	**	**	**	**	**

B) Uptake of nutrients under seedling drought conditions (F-ratios):

SV	df	Fe	Zn	Na	Ca	Mg
Genotype	20	3.33	1.43	0.93	4.96	1.08
Error	42	**			**	

Correlation studies were made among glossy sorghum genotypes in the uptake of mineral nutrients under irrigated and nonirrigated conditions (Tables 9.23 and 9.24). There was a highly significant correlation between uptake of different metals under irrigated conditions. Only a few of them showed significant correlation under water stress condition. Therefore, water stress interferes in the uptake of minerals.

Table 9.23 Correlations among assimilations of metals in glossy genotypes under irrigated conditions [** P=0.01].

	Fe	Zn	Na	Ca
Zn	0.661 **			
Na	0.662 **	0.497 **		
Ca	0.629 **	0.487 **	0.664 **	
Mg	0.689 **	0.672 **	0.830 **	0.784 **

Table 9.24 Correlations among assimilation of metals in glossy genotypes under seedling water stress situations. [* P=0.05, ** P=0.01].

	Fe	Zn	Na	Ca
Zn	0.430 *			
Na	0.170	0.194		
Ca	-0.076	0.136	0.077	
Mg	0.400 *	0.439 **	0.345 *	0.205

Determination of antinutritional elements in some glossy sorghum genotypes.

Some glossy lines were evaluated for the presence of the antinutritional factor nitrate at 45 days under irrigated conditions (Table 9.25). It was revealed that there were variations in nitrate contents among glossy lines, and that IS 5484 showed the maximum level of nitrate while IS 2312 and IS 8977 did not show the presence of this element.

Table 9.33 Determination of nitrate content (mg/g dry wt) in 13 glossy genotypes.

Genotypes	Nitrate	Genotypes	Nitrate
IS 5484	5.36	IS 2205	0.94
IS 2146	4.42	IS 5567	0.85
IS 8315	3.83	IS 5642	0.51
IS 2396	3.74	IS 5567	0.34
IS 18390	3.74	IS 2312	0.00
IS 8311	2.72	IS 8977	0.00
IS 1096	2.38		

MULTIPLE RESISTANCE

The simple morphological trait 'glossy' appears to show resistance to both physical and biotic factors like drought, various insects and diseases. This should be utilized to develop resistant sorghum cultivars. Some glossy genotypes showed resistance to more than one stress factor. For example, IS 5604, IS 4664, IS 5359, IS 4712, IS 3676, IS 5622, IS 4661, IS 1054, IS 2314 and IS 2312 showed resistance to both shootfly and drought at the seedling stage. Lines with high yield potential and a high level of tolerance to shootfly have been developed (Agrawal and House, 1982). All these lines (200) have been tested for their resistance to drought at the seedling stage (unpublished). Many glossy lines tolerant to shootfly were found to show a higher level of resistance to drought at the seedling stage, although the degree of resistance depended on the intensity of glossiness.

CHARACTERISATION AND POTENTIAL USES OF GLOSSY GERmplasm ACCESSIONS IN SORGHUM CROP IMPROVEMENT**Agronomic traits****Observations in India**

Glossy lines showed much variation in days to flowering in both the rainy and postrainy seasons. During the rainy season at Patancheru, a large number of lines from West Africa and East Africa were found to be photoperiod sensitive. During the rainy season: 126 lines were very late in flowering (95-160 days); some (103) were early in flowering (50-72 days); the maximum number of lines (221) were in the 73-94 days group. Although the maximum number of lines (422) were

(25.4-52 cm), a few (7) were in the dwarf group (75-16.4 cm) and a few had an intermediate height (16.5-25.3 cm). During the postrainy season: a few lines (14) were early (47-60 days) while a large number of lines (375) were in the intermediate group (61-86 days). 83 lines were in the dwarf group to medium height group (10.5-20 cm), while the maximum number of lines were in the tall group (20-24.6 cm).

The glossy sorghum germplasm had a normal distribution with respect to days to flowering and plant height in both the rainy and postrainy season. In the rainy season, the occurrence of more early glossy lines were observed. The glossy lines showed much diversity in agronomic traits indicating the scope of selection for a desirable combination (Maiti *et al.*, 1984).

Observation in Mexico

Sorghum lines (495) were evaluated in Marín, Nuevo León, for different agronomic traits like seedling vigor, glossy score, days to flowering, presence and intensity of waxy bloom and its intensity, plant height, peduncle exertion, panicle grain colour, glume covering and photosensitivity (unpublished). Glossy lines showed the variability in intensity of waxy bloom described by Chaterton *et al.* (1985) (Table 9.26), indicating that very few of glossy lines had waxy bloom score of 1, many of them fell in score 4. Many of the lines were also evaluated during 1983 and early 1984 and showed photosensitivity. In the early season, 132 photosensitive lines were found. In the late 1989 season, days to flowering ranged from 55 to 75. The genotypes showed much variability in seedling emergence, seedling vigor, glossy score and plant height. The majority were late in flowering (70 days, 85.6%), intermediate (61-70 days, 13.8%) and 0.5% were early <60 days). Of the lines, 41% had maximum waxy bloom, while 88% had axillary buds, 22% did not have them. The majority of the lines had more than 150 cm (72%), 25% between 101-150 cm, and 2.3% were between 51 and 100 cm. Most of the lines had the peduncle covered with an undesirable leaf sheath (58.6%), the lines, of course, showed good exertion.

Table 9.26 Distribution of 106 glossy lines in the intensity of waxy bloom in glossy sorghum at Marín, N.L., Mexico. [1=highest - 5=minimum waxy]

Scores	Number of glossy lines
1	4
2	13
3	24
4	39
5	26

Most lines had small panicles (<15 cm, 59.7%), but some had good panicle length. Fifty-six percent of the genotypes were the white grained type. A large number of glossy lines had waxy bloom scores varying from 3-5. A maximum number of lines had waxy bloom scores of 4 at the seedling stage. Very few lines

have a maximum waxy scores (1) (unpublished). The glossy trait with diverse resistance might well be incorporated in the Mexican breeding lines.

Genetic diversity

The genotypic diversity among glossy lines for agronomic traits and shoot fly resistance has been estimated following Mahalanobis D^2 (Table 9.27). The genotypes having different glossy scores were grouped into 2 minimum groups.

Table 9.27 Genetic diversity of glossy lines for agronomic and shoot fly resistance traits. [PE = Plants with eggs; DH = Plants with deadhearts]

Characters	Group A	Group B
Days to flower	(S1, S2)	(S3, S4)
Plant height, cm	(S1, S2, S3, S4)	
Panicle length, cm	(S1, S2)	(S3, S4)
100 seed weight, g	(S1, S2, S4)	(S3)
PE (%)	(S1, S2)	(S3, S4)
DH (%)	(S1, S2)	(S3, S4)

Among agronomic traits days to flower and panicle length have similar patterns of clustering, i.e. high and medium glossy groups (S1, S2) form one cluster (A) and low glossy group (S3, S4) form another cluster (B). Similar patterns were observed in shootfly resistance parameters, PE and DH%. In the case of plant height and 100 seed weight, the clustering pattern showed no relationship with level of glossiness.

Grain and fodder improvement

Means and correlations of some agronomic characters of importance for grain and fodder improvement, including days to flowering, plant height, panicle length, panicle breadth and 100-seed weight were evaluated for 513 sorghum genotypes classified according to glossy score classes (Table 9.28). Glossy genotypes were generally tall and late in flowering. Genotypes with days to flowering less than 75 days and plant height more than 250 cm have been considered for grain and fodder improvement. The results indicate that in all the cases, the desirable expressions of the traits for grain yield improvement (earliness, short stature, large panicle and high 100-seed weight) had an inverse relationship with intensity of glossiness.

The correlations among the agronomic traits in high glossy and low glossy lines based on the selection for grain, fodder and grain/fodder are shown in Table 9.29. These values indicate that in the glossy group selected for grain yield, days to 50% flowering had a negative association with panicle length and breadth, but a positive association with 100 seed weight. None of the associations were significant in less glossy groups. In the case of genotypes selected for fodder yield, plant height was significantly correlated with panicle length in high glossy groups but none of the associations were found to be significant in high and low glossy score groups. In the lines selected for fodder and grain yield, panicle length showed significant

Table 9.28 Mean values of agronomic traits within each glossy score for different selections during Rabi season in India. [* P=0.05, ** P=0.01]. Figures in parenthesis indicate the number of genotypes in each class.

Class	DF ¹	PH ¹	PANL ¹	PANB ¹	100SDW ¹
Overall					
Score 1 (267)	77.76	216.76	13.46	6.69	2.22
Score 2 (208)	76.30	212.71	4.18	6.62	3.29
Score 3 (38)	72.08	210.14	16.43	7.26	3.53
Overall (513)	76.78	214.65	13.96	6.65	3.27
Selection for grain yield potential					
Score 1 (111)	68.88	212.14	14.21	6.75	3.20
Score 2 (101)	69.03	208.16	14.94	6.81	3.29
Score 3 (23)	67.52	206.60	17.50	7.63	3.49
Overall (235)	68.80	209.86	14.86	6.87	3.27
Selection for fodder yield improvement					
Score 1 (52)	78.57	263.52	14.81	7.12	3.25
Score 2 (39)	78.15	267.07	16.21	6.92	3.42
Score 3 (7)	74.33	268.89	18.28	7.78	3.64
Overall (98)	78.04	265.38	16.66	7.10	3.25
Selection for forage and grain yield improvement					
Score 1 (31)	76.45	265.45	17.39	8.33	3.30
Score 2 (24)	78.69	270.58	19.79	7.58	3.59
Score 3 (4)	71.17	265.83	22.92	9.25	3.98
Overall (59)	76.86	267.54	18.86	8.11	3.48

DF: Days to 50% flowering; PH: Plant height (cm); PANL: Panicle length (cm); PANB: Panicle breadth (cm); 100SDW: 100 seed weight (g).

negative correlation with days to flowering and significant positive relationship with plant height. Therefore, with an increase in days to flowering, panicle length and panicle breadth got smaller. Early flowering is desirable for better panicle length and panicle breadth, which are considered responsible for grain improvement. Plant height, which is considered as a desirable trait for fodder improvement, showed a positive association with other grain yield contributing traits like panicle length, panicle breadth and 100 seed weight. This indicates that taller plants with high glossiness may be desirable for fodder improvement.

These results reveal that glossiness is not associated with deleterious traits, but rather showed significant correlations among the desirable agronomic traits like plant height, days to flowering and panicle length, both for grain and fodder improvement. Therefore, the genotypes with high glossy scores could be explored for genetic improvement for grain and fodder yields.

Genotypes with superior agronomic traits for their potential use by breeders for grain yield improvement (with < 70 days to 50% flowering) are: IS 4334 (59 days to 50% flowering), IS 4522 (56), IS 4523 (52), IS 4776 (59), IS 5139 (57), IS 5135 (47), IS 8311 (52), IS 8655 (57), IS 17815 (59), IS 18499 (52), IS 18571 (59),

Table 9.29 Correlations among agronomic traits within each glossy scores selected for potential uses. [* P=0.05, ** P=0.01]

Character	Correlations among agronomic traits	
	High glossy (score 1 & 2)	Low glossy (score 3 & 4)
a) Selected for grain		
DF vs PH	0.03	0.23
vs PANL	-0.34 **	-0.24
vs PANB	-0.17	-0.28
vs 100 SDW	0.27	0.13
b) Selected for fodder		
PH vs DF	0.21	0.41
vs PANL	0.62 **	0.07
vs PANB	0.18	-0.70
vs 100 SDW	0.15	0.06
c) Selected for fodder & grain		
DF vs PH	0.02	0.13
vs PANL	-0.39 *	-0.54
vs PANB	-0.09	-0.31
vs 100 SDW	0.26	0.33
PH vs DF	0.20	0.13
vs PANL	0.56 **	0.43
vs PANB	0.23	-0.72
vs 100 SDW	0.11	0.24

and IS 18627 (59).

Some promising germplasm lines for breeding for forage improvement are (plant height > 250 cm): IS 1054, IS 1560, IS 1560, IS 2268, IS 2282, IS 4578, IS 4632, IS 4675, IS 5047, IS 5172, IS 22196, IS 6566, IS 7891, IS 16534, IS 16088, IS 16528*, IS 2185*, IS 166611*, and IS 166640* (* promising forage yielders).

For dual purpose, forage and grain (plant height > 250 cm and days to 50% flowering < 70): IS 1054, IS 1560, IS 2185, IS 2268, IS 4578, IS 4632, IS 5172, IS 5553, IS 6566, IS 7891, IS 16088, IS 16528, IS 16611, IS 16614, IS 16614, 16640, and IS 22196 are suggested.

Similar studies were undertaken for Kharif season data on high and low glossy lines (Table 9.30). The mean values reveal that low glossy groups had agronomic desirability as observed in Rabi season data. The correlations between days to flowering and plant height were significant among all the genotypes and among the subgroups selected for grain and forage in high and low glossy lines. Glossy sorghum lines could be favourably utilized for fodder improvement. Since glossy traits are also associated with resistance traits, the genotypes of high glossy class can be selected and tested in semiarid situations of the world especially in India and Africa to assess their genetic potential for fodder and grain production.

Table 9.30 Mean values and correlations among some agronomic traits of glossy sorghum genotypes in different score classes during Kharif season. [* P=0.05, ** P=0.01]

Classes	OVERALL			GRAIN		FORAGE		r	
	Mean	PH ¹	r	Mean	r	Mean	r		
	DF ¹	PH ¹	r	DF	PH	DF	PH		
Overall	89	341	0.75 **	70	286	0.62 **	90	349	0.78
Score 1	89	346	0.81 **	71	298	0.53 **	89	348	0.81**
Score 2	89	335	0.70 **	69	277	0.61 **	91	349	0.76*
Score 3	86	332	0.77 **	66	264	0.68 **	90	352	0.74**

DF = days to flowering, PH = plant height, cm.

growth analysis and productivity of some glossy sorghum genotypes under irrigated and rainfed situation in Mexico

Fifteen glossy sorghum genotypes (IS 5604, IS 1034, IS 4663, IS 18390, IS 2205, IS 5484, IS 8315, IS 5642, IS 1096, IS 8977, IS 5587, IS 4776, IS 5622, IS 5567, IS 16567) were evaluated for growth analysis and fodder productivity under irrigated and rainfed situations in Nuevo Leon, Mexico.

Growth pattern: Plant height = growth was slow under nonirrigated conditions, but under irrigation plants grew faster. Leaf area = under irrigation and nonirrigation, leaf area showed first a gradual and then sharp rise up to 76 days, but under rainfed condition, growth was reduced. Net assimilation rate (NAR) = NAR was higher under irrigation than rainfed conditions. Under the rainfed situation, IS 5567 showed maximum NAR and IS 8315 the minimum. Under the irrigated conditions, IS 8315 showed maximum NAR and IS 4776 the minimum. The genotypes showed sharp increment in NAR from 61 to 76 days under irrigation. Under rainfed situation, IS 5567, IS 5604 and IS 5642 showed similar growth pattern in the irrigated situation. Under irrigation, leaf number, leaf dry matter and stem dry matter did not show significant differences (P = 0.05) at 31, 46, 61 and 76 days, but plant height showed differences. These variables showed significant differences among stages (P=0.05) and interaction, genotype x stage were also significant (P = 0.05). Under the rainfed situation, leaf number, leaf dry weight and plant height showed significant differences among genotypes (P = 0.05), but stem dry matter and leaf area did not show differences. These variables showed differences among stages and genotypes x stages interaction. Dry matter partition (DMP) = DMP showed large differences among genotypes under both irrigated and nonirrigated conditions. Under nonirrigated conditions, IS 5604, IS 1034, IS 4663, IS 1096, IS 8977, IS 4776 and IS 5622 showed similarity in DMP (70% in stem, 20% in leaf and 10% in panicle), but for IS 18390, IS 2205, IS 5484 and IS 5567 DMP in the stem was 70%, and for IS 5484 only 40%. IS 8315 showed maximum dry matter proportion in stem (70%). In IS 18390 and IS 2205, dry matter in leaves were 44 and 43% respectively, with the minimum in IS 5567 (30%). The proportion of dry matter in the panicle was maximum in IS 5484 (20%) and minimum in IS 5642. Under the rainfed situation, the genotype beha

viator was similar in majority of the genotypes. IS 18390, IS 2205, IS 5484 and IS 5567 showed different behaviour. Fodder yield (Table 9.31) under rainfed conditions IS 5587, IS 5604, IS 5484 and IS 4776 are recommended for forage and grain production in semiarid India and Mexico.

Table 9.31 Average fodder yield (dry matter, tons/ha) of some glossy sorghum lines in Nuevo León, México.

Genotype	Fodder yield (dry matter, ton/ha)	
	Rainfed	Irrigated
IS 5604	16.20	15.16
IS 1034	12.81	13.95
IS 2146	10.44	8.15
IS 4663	13.75	12.36
IS 18390	13.84	12.48
IS 2205	13.02	18.00
IS 5484	16.17	12.54
IS 5642	12.78	12.92
IS 5587	18.49	19.26
IS 8315	11.37	13.11
IS 1096	11.43	12.14
IS 5567	13.18	13.36
IS 4776	14.00	14.30

Utilization of glossy lines in sorghum crop improvement

Two easily identifiable traits, the trichomes and glossiness are highly inheritable with simple inheritance and additive in their effects in the shootfly incidence (Maiti and Bidinger, 1979; Maiti and Gibson, 1981; Gibson and Maiti, 1981). Adopting this technique Agrawal (1984, personal communication) made good progress in breeding for shootfly resistance since it is an easily identifiable trait during seedling stage, the early generations segregating materials can be evaluated based on this trait and at the later stage can be tested under shootfly pressure to verify their reaction.

In general, glossy lines showed higher recovery percentage after release of stress than the nonglossy plants. Some nonglossy lines showed good recovery. Therefore, the resistance mechanism cannot be ascribed solely to the glossy character, other factors, as yet unidentified, seem to play a role in drought resistance. Breeders at ICRISAT have started to backcross to the agronomically elite materials, the traits, trichomes and glossy leaves, as many of the elite lines lacked the resistance traits.

The glossy lines were generally poor agronomically, but some lines have been identified as having good agronomic traits: IS 4663, IS 4405, IS 5642, IS 3962, IS 4776, IS 5567, IS 4473, IS 2394, IS 1096, IS 2280, IS 5621, IS 5067, IS 6942, IS 4661, IS 2314 and IS 1054 (Rodríguez-Sandoval, 1991).

CONCLUSIONS

Sorghum genotypes could be easily distinguished into 2 distinct morphological types, glossy and nonglossy lines at the seedling stage. The glossy lines vary widely in seedling morphology, intensity of glossiness and waxy surface. About 85% of the glossy lines show presence of nonglandular microscopic hairs, trichomes on the surface. Some sorghum lines from germplasm with trichomes and glossy traits showed a higher level of resistance to shootfly. Some lines are resistant to stem borer also. Both trichomes and glossy trait are linked and have a large repercussion on shootfly resistance, thereby improving the prospects for development of cultivars with increased resistance. Glossy lines also showed variability in biochemical traits which need to be related to their resistance mechanisms to various stresses.

Some glossy lines have better tolerance to seedling drought, but there were some lines falling in the susceptible group. Most of the glossy lines have been identified as land races belonging to the race Durra and predominantly distributed in central India. Some of them are exotic in origin and show diversity in geographical distribution. Though many of the glossy lines are poor in agronomic traits, some lines with desirable agronomy were identified. These lines could be recommended for forage and grain improvement in the semiarid tropics.

Insects, pests and the lack of adequate moisture supply are the major barriers in improving sorghum crop production in SAT areas. For a long time, physiologists and breeders have been testing for simple characteristics which reliably predict drought resistance. At the same time, physiologists in collaboration with breeders and entomologists are working together to identify simple morphological traits related to insect and drought resistance. The use of trichome and glossy trait proves to be the most effective and reliable selection criteria in the breeding for shootfly maintenance, and probably drought resistance. The variability in several biochemical traits like HCN, chlorophyll (a, b, and total), water use efficiency and water contents among glossy sorghums could be correlated with resistance mechanism to different stress factors.

PROBABLE PLANT TYPE CONCEPT IN SORGHUM

The term 'plant type' include a set of morphological characteristics contributing to higher yield in sorghum. Since sorghum is grown both under optimal and suboptimal conditions in the semiarid tropics and temperate regions, concepts of better plant type in a particular situation differ with region. Plant type concept could be investigated for sorghum with some modifications. The following morphological characteristics in sorghum deserve particular attention:

Short stiff culms

For efficient utilization of soil moisture in rainfed conditions, short and stiff culms of 1-2 m height are desirable. A short sorghum plant may make more lodging and be stalk root resistant. A strong stem with intensity of mechanical tissue-sclerenchyma offers resistance to lodging stalk rot and is also insect resistant.

Stout and juicy stem may prove susceptible to insect and disease. For this, only a part of the internode should be covered with leaf sheath. A single culm is desirable for high yield.

2. Erect leaves

Erect leaves with a stiff midrib forming an acute angle with the stem permit deeper penetration and even distribution of light which may result in increased photosynthesis. A waxy coating on the leaf surface may reduce transpiration in dryland agriculture. Glossy leaves with thick cuticles and dense trichomes may be associated with insect and drought resistance.

3. Root system

A profuse root with a number of deep roots is ideal in rainfed agriculture. Long seminal roots are desirable for the initial establishment of seedlings. Presence of pericyclic lignification may be associated with drought resistance and resistance to root rot. A higher number of nodal roots may be disadvantageous to the plant. A smaller number of nodal roots arising from basal nodes are required for mechanical support as well as absorption of soil moisture during the grainfilling period. Under optimum soil moisture, the roots may need to be distributed at shallower depth.

4. Panicle

A panicle with large number of intermediate or bold grains and good exertion is desirable for high yield. A large and compact panicle may provide favorable environments for insect and disease attack in the tropics. Therefore, a loose panicle with long primary branches and a large number of grains is ideal in these environments. Large seeds should be exposed, and up to 75% of them should be covered with glume. Bold seed associated with white grain is desirable for quality with good stand establishment.

GENERAL COMMENTS

Traditional yield advances in different crops have been achieved by the combined efforts of management specialists, plant pathologists, entomologists and plant breeders. To accelerate this progress, biochemists and plant physiologists have recently joined the team. A thorough knowledge of basic plant sciences and an understanding of plant growth and crop production would provide a key to identify the physiological, morphological and architectural components of the germplasm with superior yield. For this, the proper exploitation of the rich sorghum germplasm resource and cataloguing the resources to make them available all over the world is a basic prerequisite to maximize the crop yields.

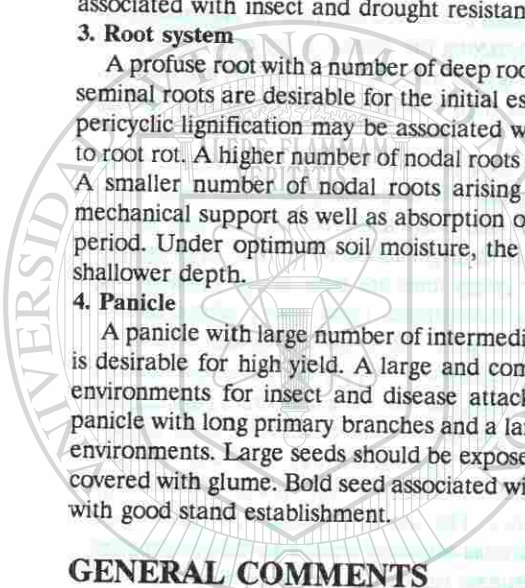
The next step is identification of resistance traits and their proper utilisation in breeding to keep up the yield potential. This knowledge in turn can be used to increase yield potential.

As discussed in earlier chapters, the formulation of simple techniques for identification of sorghum lines with different resistance was attempted. Some sorghum germplasm showing multiple resistances have been identified. Breeders may attempt to transfer the resistance genes to elite lines by adopting a suitable

method and incorporating resistant traits in early generations. Progenies of crosses between resistant and susceptible elite lines could be tested at early germination without taking recourse to any plant protection measures and selected progenies advanced may have the potential to accumulate resistant genes. These advanced lines could be adaptable to a wide range of environments and resist drought, pests and diseases.

A superior genotype with multiple resistance should be selected, developed and tested under different environments to exert selection pressure. Then the breeder should incorporate multiple resistance into elite lines by establishing the corresponding genetic inheritance.

Most of the advances in crop production in the advanced countries have been derived from empirical breeding and management research. Research efforts have been directed to develop highyielding crop varieties under good crop management condition, but very little fundamental research on plant responses to favorable environments and the mechanism of adaptation under adverse conditions has been done. Some basic questions remain. What are the traits responsible to tolerate drought, salinity, low phosphate, heat, etc. What is the biochemical basis for these tolerances and how are they genetically controlled?



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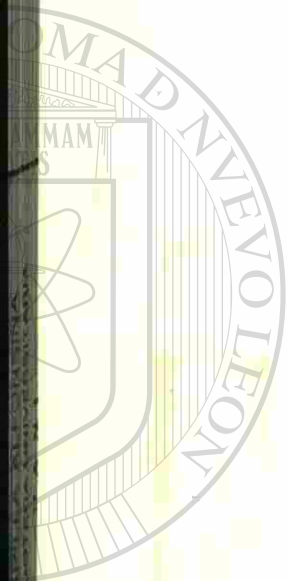
ERRATA

Corresponding figure: corrected version.

Figure 4.19 Transverse section of a culm, giving orientation and development of the tissue of the leaf sheaths encircling the stem.

Figure 4.20 Transverse section of a pseudostem, depicting little mechanical tissue, small and large vascular bundles in the peripheral region.

Figure 4.21 Transverse section of stem showing heavy mechanical tissue in the peripheral region and around the vascular bundle.



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