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A Guide to Sorghum Breeding

Second Edition

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FOREWORD

Through the ages sorghum has been a vital source of food for millions of people; in the semi-arid tropics (SAT), it is often the principal means of survival. In recent years, steadily expanding populations have brought increased demands for this dependable staple, but in the SAT, where more than half the world's sorghum is grown, environmental conditions severely limit production.

The small farmer is the first to feel these pressures of increased demand and limited supply. Cereal scientists have made substantial advances in crop yields of rice and wheat with new varieties and technology—but most of that progress has been made where growing conditions are favorable. Improvement of sorghum yields is a more difficult task. It is often grown on poorer soils by farmers who have little control of moisture or availability of fertilizers and other inputs that will boost yields. But as a crop sorghum offers proven versatility, hardiness, dependability, and stability of yield under very adverse conditions. Because it has demonstrated its adaptability over such a wide range of cultures and climates, it offers great potential for supplementing the world's food resources.

Millions of people now eat sorghum as a staple food (*chapati* or *roti* in India, *injera* in Ethiopia, *tortillas* in Latin America, etc.). It also is used as feed for animals and is an industrial raw material. Other uses include processing for beer and preparation of other local drinks; its stalk provides fodder, fuel, shelter, sugar, and syrup.

Because of its importance as a staple cereal for millions of the poorest people of the semi-arid tropics and because of its potential for vastly increased production to help feed the undernourished of developing nations, sorghum is one of the five crops that ICRISAT has a mandate to improve. In compiling this book on *Sorghum bicolor* (L.) Moench, Dr. Leland House, former principal sorghum breeder and program leader at ICRISAT, and presently manager of the SADCC/ICRISAT Cereals Improvement Project for southern Africa, has utilized the knowledge and experience gained from some 25 years' work with this crop with numerous experts and organizations worldwide.

It is our hope and expectation that this book will be a valuable guide, particularly to young scientists and senior technicians, in enhancing improvement of this crop so important to the health and well-being of millions.

L.D. Swindale
Director General

ABOUT THIS BOOK

The content and organization of this guide have been developed through several years of field use in draft form; it has been modified and expanded based on this experience.

No claims are made for speedy, spectacular performance, nor are there fixed formulas for successful sorghum production. Rather, the main objectives are to guide in problem identification and basic descriptive analysis, with working examples of breeding theory applied in the field. A systematic breeding approach is recommended. Intended readers are the crop specialists, field technicians, scientists, and students interested in field-oriented sorghum improvement. It is hoped that these readers, and others at national program-planning levels, will also find a broader perspective for analyzing and structuring their overall crop improvement work.

Five general topics are covered:

Section 1 is mainly descriptive, providing background on the current status of sorghum and some of its basic characteristics. Some of its earlier history is outlined, and sorghum's classification systems are listed along with information showing its worldwide distribution.

Section 2 focuses on the sorghum plant, its growth stages and morphology. Here emphasis is on how the plant develops from seed to maturity. Special characteristics of the sorghum plant are noted, with particular attention to the interests of the sorghum breeder.

Section 3 provides a relatively detailed look at plant genetics from a field technician's viewpoint. The emphasis is on applied uses of genetics as a working tool. Genetics of sorghum completes this section.

In Section 4, the reader moves directly to the basic methods and procedures of crop improvement—the world collection of sorghums and their use, pedigree nomenclature, field techniques in crossing sorghum, procedures to screen for various yield-limiting traits, and breeding for food quality.

A wider focus is found in Section 5, which outlines the role, organizational scheme, and operational plans for high-quality seed production and distribution. The aim is to show how crop-improvement workers can integrate their work—from research and development through production and marketing of high-quality seed and on to the farmer.

As noted, draft versions of the book have been used for several years in training work, and the author is aware of many of its limitations in covering so broad a subject. While few formal citations and references are listed here, readers are invited to consult ICRISAT's published sorghum bibliographies and other services of the Institute's Sorghum and Millets Information Center.

Readers are encouraged to provide additional comments and criticism that might be useful in later revisions or supplements. Certainly, those working actively in crop production and research now under way will be able to make rich contributions for future field-oriented publications.

ACKNOWLEDGMENTS

This book has been in process for many years. It was begun in India as part of the Indian Agricultural Program (IAP) of The Rockefeller Foundation. Staff of this program participated in the All India Coordinated Sorghum Improvement Project of the Indian Council of Agricultural Research (ICAR). Many photographs came from stations of the ICAR program and from stations of the departments of agriculture of the various states in India. Section 5, on the seed industry, was organized from the writings of Drs. Guy B. Baird, Johnson E. Douglas, Wayne H. Freeman, and Leland R. House—all while with the IAP.

The work on this book expanded as part of the training effort of the Arid Lands Agricultural Development Program (ALAD) of the Ford Foundation. A substantial portion of the section of genetics was written by Dr. Geoff Hawtin, then on the staff of the Interntional Development Research Centre of Canada, stationed with ALAD, and now at ICARDA, Aleppo, Syria.

I deeply appreciate Dr. L.J.G. van der Maesen's contributions to the section on taxonomy and Dr. J.P. Moss's revision of the section on basic genetics in this second edition, as well as significant contributions by scientists in the ICRISAT Sorghum Improvement Program to the subsections on development of the screening procedures and breeding for food quality in Section 4, which are new in this edition.

Special thanks are also due to Robert C. Lommasson, Kit W. Lee, and the Sorghum Physiology program of the University of Nebraska for photographs and particularly the plates of photographs on the development of the floral bud and panicle.

Jim Bemis, then editor with CIMMYT, contributed substantially to the first edition of this book in 1979 while on contract with ICRISAT, as did Gloria Rosenberg, former Research Editor at ICRISAT, who also edited this second edition. I also appreciate the considerable contribution by the staff of ICRISAT's Information Services to the final preparation and printing of both editions. Finally, my thanks go to ICRISAT itself for the financial and institutional backing that made this book possible.

The input of the people and institutions mentioned above, and the many more not mentioned, should help ensure that this book will make a contribution to sorghum breeding.

L.R.H.

SECTION 1
THE SORGHUM PLANT

ITS BASIC USES, CHARACTERISTICS, AND DISTRIBUTION

Section 1 is designed to show how the crop is used; where it is grown in terms of climate and geographic distribution; and its production, origin, and classification. The discussion is not exhaustive; classification changes with time, and there is not a full consensus among sorghum breeders on a classification system; on the other hand, the differences are not great. Knowledge about the origin and distribution of sorghum increases each year. This discussion is an attempt to introduce the reader to sorghum, with emphasis on information of interest to breeders.

Sorghum Uses

Sorghum grain is used for human food and as feed for animals; the plant stem and foliage are used for green chop, hay, silage, and pasture. In some areas the stem is used as building material, and plant remains (after the head is harvested) may be used for fuel.

An unleavened bread prepared with flour ground from the grain is one of the most common foods made of sorghum. Sometimes the dough is fermented before the bread is prepared. Generally, a pearly hard white grain is desired for this purpose. Sorghum is also boiled into a porridge or gruel. Beer is commonly made of the grain in many parts of Africa, often with grain of various colors. There are "specialty" sorghums, such as pop sorghum and sweet sorghum, that can be parched and eaten. These specialty sorghums are frequently grown as borders of large fields.

Quality sorghum grain is usually hard (vitreous), white with a pearly luster, bold and round, with a thin seed coat (pericarp), and without a colored subcoat (testa). However, there are many variations in color, hardness, and shape of the grain used for food in different parts of the world. The quality of sorghum protein is deficient, like that of several other cereal crops, because of a low concentration of the essential amino acid, lysine. High-lysine sorghum types have been found growing in the Wollo district of Ethiopia, and several other sources have now been identified. Breeding programs are actively studying the possibility of incorporating this trait into their better lines and varieties for farmer use. Many problems are involved, probably limiting high-lysine sorghum to special uses.

Sorghum used as a feed grain is generally softer than that used for food grain; its grain is often colored. It is seldom fed without coarse grinding or breaking—other processes involve various soaking procedures, flaking, and popping. The purpose is to expose a larger portion of the seed to the animal's digestive enzymes. If not treated, some grain (when used as feed) will pass through the animal undigested.

The sorghum plant makes good feed. It can be chopped for silage or fed directly to the animals. Sudangrass is used as pasture and made into hay. The stover—the portion remaining after the head is removed—is often used as hay. This, however, is poorer in quality than stover from sorghum managed as a feed crop.

Cyanide can be produced in poisonous quantities by some sorghum and sudangrass. The cyanide concentration is greatest in seedling plants and declines as the plant grows: it is low after 30 to 40 days of growth and virtually absent just before heading. The concentration of cyanide is most serious in new growth following cutting. The greatest danger occurs if regrowth is damaged by frost. The cyanide problem can be managed by careful

attention to selection of varieties low in cyanide, and by proper grazing. Presence of cyanide need not be a serious restriction to the use of sorghum forage for feed.

Basic Characteristics

Yield Potential

Sorghum has a high yield potential, comparable to those of rice, wheat, and maize. On a field basis, yields have exceeded 11 000 kg/ha, with above average yields ranging from 7000 to 9000 kg/ha where moisture is not a limiting factor.

In those areas where sorghum is commonly grown, yields of 3000 to 4000 kg/ha are obtained under better conditions, dropping to 300 to 1000 kg/ha as moisture becomes limiting.

Adaptability

Sorghum adapts to many environments, requiring 90 to 140 days to mature. Highest yields are usually obtained from varieties maturing in 100 to 120 days. Such grain sorghum usually has a grain-to-straw ratio of about 1:1. Varieties maturing earlier may not yield quite as much because of the reduced growing period; late-maturing varieties tend to put on foliage and make less grain (the grain-to-straw ratio may run as high as 1:5). Better yields of such late varieties commonly average 1500 to 2000 kg/ha, compared with 4000 to 5000 kg/ha or more for 100- to 120-day types.

Fertilizer Response

Fertilizer response varies for different varieties. Many traditional varieties developed in low fertility and droughty situations produce 6 to 10 kg grain per kg applied nitrogen, whereas varieties responsive to high levels of fertility produce 20 to 40 kg grain per kg applied nitrogen. Locally available lines should be studied to determine their responsiveness to fertilizer.

Water Relations

Sorghum is usually grown under hot, dry conditions. Compared to maize, sorghum has a more extensive and fibrous root system. The plant roots penetrate a greater volume of soil to obtain moisture. Fertilizer, even under low rainfall conditions, encourages root development; hence the roots are able to extract moisture from a greater volume of soil. The increased moisture then available to the plant, along with the improved fertility, stimulates higher yields. Sorghum requires less moisture for growth than some other cereal crops: studies show that sorghum requires 332 kg of water per kg of accumulated dry matter; maize requires 368 kg of water; barley, 434 kg; and wheat, 514 kg. Sorghum tends to "hang on" during the dry period and resumes growth with the return of rain.

The water requirement of sorghum increases as the plant grows, reaching a peak during the flowering period; after this time, the moisture consumption decreases. At peak consumption, sorghum uses about 6 to 7 ha mm of water per day. Sorghum also withstands wet extremes better than do many other cereal crops (especialy maize: sorghum continues to grow, though not well, in a flooded condition; maize, by contrast, will die). Sorghum also has some tolerance to salt and aluminum toxicity.

Temperature Relations

Sorghum will make grain even when temperatures are high. Crossing may be difficult if temperatures are 40°C or more, with relative humidity of 30% or less; but a crop can be obtained if moisture is available (especially if available prior to and during the flowering period). Floral development and seed set are normal at temperatures of 40 to 43°C and at 15 to 30% relative humidity, if soil moisture is available. Sorghum is not as tolerant to cool weather as maize. Sorghum grows slowly at 20°C, but germination and growth will occur in some varieties with temperature as low as 12°C.

Plant Protection

Insects: Insects are a serious problem in the cultivation of sorghum. The shoot fly (*Atherigona soccata*) can severely damage the crop at certain times of the year. A number of stem borers infest the crop. A small fly, "midge" (*Contarina sorghicola*), occasionally is very damaging to seed set. (Midge lays its egg in the floret at the time of flowering and the maggot feeds on and destroys the developing seed. A crop can be completely lost because of this insect.) These problems can be controlled by use of insecticide. For example, in experimental crops, Furadan or Thimet can be used against shoot fly,

Endrin or Sevin against borers, and 5 to 10% BHC dust against midge. Other appropriate insecticides are available.

Diseases: A number of diseases are of major economic concern. Most important among these are grain molds; downy mildew (*Peronosclerospora sorghi*); and charcoal rot (*Macrophomina phaseolina*). Anthracnose (*Colletotrichum graminicola*), downy mildew, and maize dwarf mosaic virus are among the more important diseases in the Americas. Breeding for resistance is the best method of control.

Weeds: The parasitic higher plant *Striga* (witchweed) is a major limiting factor in parts of Africa and India. *Striga hermonthica*, found from Tanzania to Ethiopia and westward across the African continent, is the most important species. *Striga asiatica* is found in central and southern Africa and is the most important species in India.

Bird damage: Birds can be a serious problem, especially when the crop is an introduction or a variety that matures much earlier or later than the local type. Bird damage tends to become less as acreage increases, or if the crop is sown so as to mature along with some other crop in the area.

Nematodes: These have rarely been found to limit yield but may become a problem if a field is planted continuously to sorghum for several years.

Current Production Data

Estimates for the production of sorghum are complicated because the reporting systems of a substantial number of countries combine data for both sorghum and millets. Information presented here relates primarily to sorghum but includes the millets at times (Table 1.1).

Worldwide, the area sown to sorghum increased from 38.5 to 43.9 million ha from 1961-65 to 1976. Average yields for sorghum for the world increased from 918 to 1179 kg/ha during this period, while total production has increased from 35.3 to 51.8 million metric tons. Among the major cereals, sorghum ranks fifth in area sown, following wheat, rice, maize, and barley. Average yields are lower than all other grains reported, except millet. The lower average yields are primarily a result of the hot, dry conditions where sorghums are most commonly grown, rather than a reflection of the plants' capability. Sorghum will outyield maize in some environments when well managed; production areas are increasing dramatically in many locations, including some traditionally maize-growing areas. In Latin America, for example, the area sown to sorghum has increased about threefold: from 1.5 to 4.2 million ha. This increase is attributed in large part to the virtually complete change from cultivation of varieties to the cultivation of hybrids.

Table 1.1: Yields (kg/ha) for the major cereals of the world (1976).

Crop	Average yield (world)	Crop	Average yield (world)
Maize	2829	Wheat	1774
Rice	2428	Rye	1683
Barley	2030	Sorghum	1179
Oats	1666	Millets	707

Sorghum Domestication

Origin

It is difficult to determine when and where domestication occurred (de Wet et al. 1970). Murdock (1959) has suggested that the Mande people around the headwaters of the Niger River may have domesticated sorghum. Doggett (1965a) indicated that archaeological evidence suggests that the practice of cereal domestication was introduced from Ethiopia to Egypt about 3000 B.C. It is possible that domestication of sorghum began about that time. De Wet et al. (1970) studied archaeological reports but found only meager information about sorghum.

De Wet and his colleagues suggest that sorghum had a diverse origin and probably arose from *Sorghum verticilliflorum*. *S. arundinaceum* is a grass of the tropical forests, and *S. aethiopicum* and *S. virgatum* are found in desert regions. These habitats are outside the major sorghum areas and probably contributed less to its domestication. *S. verticilliflorum* is usually found in areas where sorghum is cultivated. There is tremendous variation in *S. verticilliflorum*; and it, as well as the other wild species, readily crosses with cultivated sorghum. It yields well and was probably collected and used before the advent of agriculture.

Snowden (1936) and Porteres (1951) suggested that races durra, guinea, and caffra are closely allied and may have arisen from *S.aethiopicum*, *S. arundinaceum*, and *S. verticilliflorum*, respectively. This, however, is difficult to demonstrate experimentally. Morphological differences between races may have

arisen because of ethnic isolation. Caffra is widely grown in Bantu Africa, while durra is not found there. Caudatums are most common in central Sudan, and Guinea corns are found primarily in West Africa. Distribution indicates that the races caffra and caudatum were derived from *S. verticilliflorum*, and that durra possibly could have come from *S. bicolor*. Guinea corn is quite distinct, but it is questionable that it could have come from *S. arundinaceum* (which is a grass of tropical forests and not found where sorghum is extensively cultivated).

Introgression studies indicate that cultivated sorghums probably developed through disruptive selection (Doggett 1965b). Crossing easily occurs between wild and cultivated types; however, these types form distinct populations. It is speculated that, as man began to select, there was substantial gene flow between improved and unimproved types. This gene flow would decrease as field sizes became larger. The selection by man and nature would provide a disruptive force resulting in diverse populations (polymorphic populations). These disruptive forces have been continuously active through time (and are still active), influencing cultivated and wild populations. Most intermediate forms do not exist long in nature: those backcrossed by cultivated crops would tend to contribute genes in the direction of cultivated types; and those backcrossed by wild types would tend to contribute genes to the wild population. Polymorphic populations would tend to be maintained and change over the years. New forms would arise, leading to the types of sorghum now in cultivation. Ethnic isolation would help this process.

The process of domestication involved a change in several characteristics of the plant. A tough primary axis (rachis) and persistence of the sessile spikelet were probably introduced early in the process. It is likely that the transformation of a loose and open inflorescence into a compact type involved several changes: first, an increase in the number of branches per node; second, an increase in the number of branches per primary inflorescence branch; and third, a decrease in the internode length on the rachis. An increase in seed size also was probably a product of domestication, the seed becoming large enough to protrude from the glumes.

Early Geographic Spread

When and how sorghum spread from Africa is a matter of conjecture. Durra types today extend continuously from Ethiopia, along the Nile to the Near East, and across India to Thailand. The durra types were probably introduced to Arabia as early as the Sabian Empire (1000 to 800 B.C.), and later spread to the Near East along trade routes. Snowden (1936) provides the dates for most of the following discussion.

Extensive trade routes (by land and sea, around the Arabian Sea and the East Mediterranean area, as far as China) date far back into antiquity. Sorghum probably reached India by both land and sea routes. Its cultivation in India is mentioned in legends that date back to the first century A.D. It is not a very old crop in India, as its Sanskrit name, "Yavanala," means reed barley or reed grain, indicating that sorghum probably followed barley into India.

The absence of sorghum from excavation sites in the Near East indicates that the crop came fairly late to this area. Possibly sorghum was introduced there about the same time it appeared in Italy. Pliny recorded (in approx. 60 to 70 A.D.) that the crop was introduced into Italy from India.

Distribution suggests that *S. bicolor* was probably introduced into China from India about the third century A.D. The presence of durra types in Korea and adjacent Chinese provinces suggests that it may have been introduced there via the ancient silk routes from Asia Minor.

Sorghum is relatively new to the Americas. It was first introduced into the United States in 1857, and was extensively used into the early 1900s for syrup (Doggett 1965a). It is now an important grain crop in several of the western states. Its cultivation in Central and South America has become significant only since 1950.

Taxonomy

Species Classifications

Sorghum has been variously classified. The following historical outline is taken from Snowden (1936): Pliny (in *Historiae Naturalis*) was the first to give a clearly identifiable written description of sorghum. Apart from this, there appears to be little written about sorghum until the 16th century, although Crescenzi mentions sorghum in some writings in 1305 A.D. Ruel (1537) refers to sorghum as *Milium saracenaceum*. Fuchs (1542), Tragus (1552), Scaliger (1557), Lobel (1576), and Dodoens (1583) mention sorghum. Dalechamps (1586) illustrated a sorghum that he called *Milium indicum sive melica* Matthio. Porta (1592) refers to the plant of Pliny as

Milium indicum, but also refers to the loose-panicle, white-seeded type as *Milium aethiopicum*, which is probably the same as that mentioned by Belon in 1553 as having come from around Cilicia (in the northeast area of the Mediterranean, primarily in Turkey). Matthioli (1598) gave illustrations of his sorghum and referred to it as *Milium indicum* Pliny. The number of references increased substantially after this period, and only a few are of interest here.

Besler (1613) illustrated two varieties, the first under *Sorgho* as *Melica italorum* and the second as *Sorghum fructu albo*. Caspar Bauhin (1623) described a number of *Milium* species using the names *Milium subrotundo semine* for the type described by Pliny. Parkinson (1640) included all sorghums under *Milium sive sorghum*. Hermann (1687) described two other species: *Milium indicum arundinaceo caule granis flavescentibus* and *Milium indicum arundinaceo caule granis nigris*. Breyne (1689) described several species, and Pontedero (1718) recorded a large number of sorghums under *Milium*. He was followed by Micheli (1729), who used the generic name *Sorghum*. Alpino (1735) described a type as *Dora* that later was identified as a durra. In 1737 Linnaeus described two species of sorghum, one as *Holcus glumis glabris* and the other as *Holcus glumis villosis*.

For valid names, modern taxonomy looks back only as far as Linnaeus' *Species Plantarum* (1753). In that work, Linnaeus described three species of cultivated sorghum: *Holcus sorghum*, *H. saccaratus*, and *H. bicolor*. Mieg (1777) referred to sorghum as *Holcus dora*; Forsskal (1775), as *Holcus durra*; Persoon (1805) created the name *Sorghum vulgare* for *Holcus sorghum* L. and *Holcus dora* Mieg. Forsskal described *H. dochna* in 1775, and Arduino (1786) described *H. cafer*, which had arrived in Italy from South Africa. Moench (1794) established the genus *Sorghum* and made the combination *Sorghum bicolor*. Our present generic and species concepts of *Sorghum* agree with the definition established by Moench, and all specific names described above are now referred to as synonyms of *S. bicolor* (L.) Moench.

Koch recorded *Sorghum halepense* in 1848. Brotero (1804) recognized the similarity between sorghums and *Andropogon* and placed them in that genus. He used the name *Andropogon compactus* for *H. sorghum* L. and *Andropogon sorghum* for *H. bicolor*. Roxburghii (1820) also referred to sorghum under *Andropogon*. Steudel (1854) described an *Andropogon subglabrescens and Andropogon drummondii*, both now considered synonyms of *S. bicolor*. Before Steudel's work, the various distinct types of sorghum were considered separate species. Alefeld, in 1866, and Koernicke, in 1885, adopted the system of subordinating all the cultivated sorghums as varieties of one species, *Andropogon sorghum*, considered to have been evolved from the wild species *Andropogon halepensis*.

Chiovenda (1912) reworked the sorghums and divided them into four groups under the genus name *Sorghum*. Piper (1915) discussed thoroughly the status of wild sorghums, still named *Andropogon* spp. Stapf (1917) also reworked the classification of sorghum, using the word *Sorghum* as the genus name. He also used the word *Eu-sorghum* to represent the "true sorghum," the other group being the *Sorghastrums*.

The most detailed classification of *Sorghum* was made by Snowden (1936, 1955), whose work stands as a tremendous contribution and remains useful to scientists today. He described 31 cultivated species and 17 related wild species. Snowden recognized that the cultivated sorghums could be considered races of one vast species, but he gave species status to the 48 different types to stress the fact that they are well defined by a number of distinct characters. At present his species are more appropriately considered to be races of one species.

Snowden (1936) later subdivided the sorghums into the following sections, subsections, and series, leaving *Sorghastrum* as a separate genus to contain more distinct types.

Sect. *Eu-sorghum* Stapf emend. Snowden
- Subsect. *Arundinacea* Snowden
  - Series *Spontanea* Snowden (10 wild species)
  - Series *Sativa* Snowden (31 cultivated species)
- Subsect. *Halepensia* Snowden (4 wild grasses)

Sect. *Para-sorghum* Snowden (8-10 annual and perennial grasses)

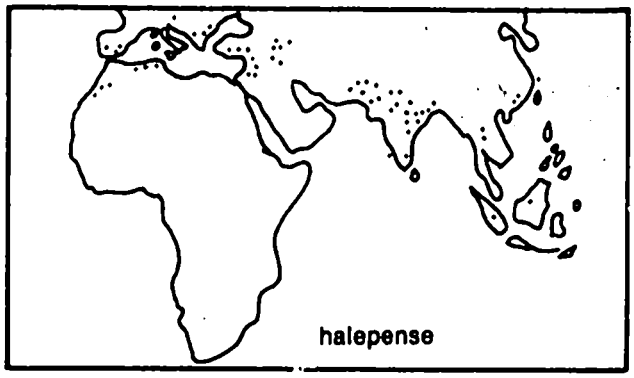
De Wet et al. (1970) described the various groups of sorghum and their distribution (Plate 1). And in 1978, after two decades of biosystematical research, de Wet reviewed the present status of the sorghums, improving on his own earlier classifications (de Wet and Huckabay 1967; de Wet et al. 1970). Quoting Garber (1950), de Wet acknowledges the following five sections of *Sorghum*:

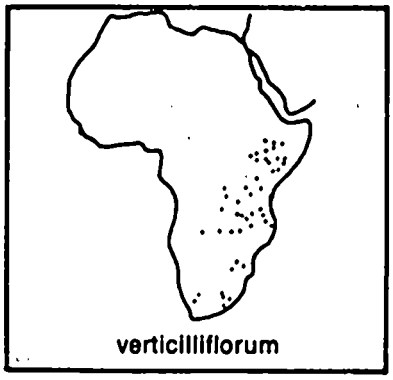
Sorghum Sect. Stiposorghum
Parasorghum
Sorghum
Heterosorghum
Chaetosorghum

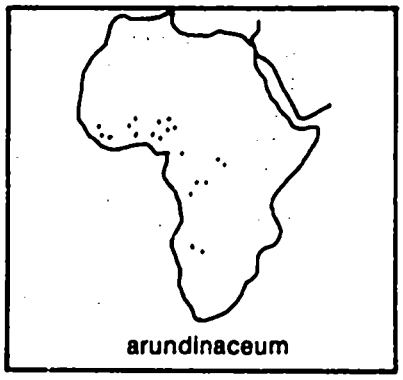
The section *Sorghum* (= *Eu-sorghum* Stapf emend. Snowden) includes annual cultivated

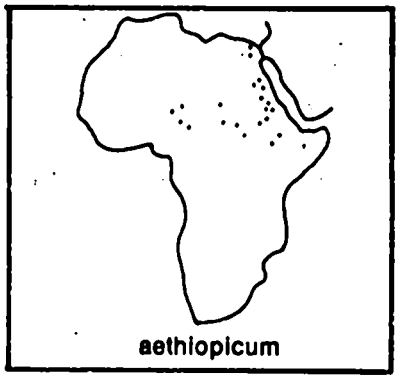
PLATE 1. DISTRIBUTION OF SORGHUM SPECIES AND RACES.

Wild:

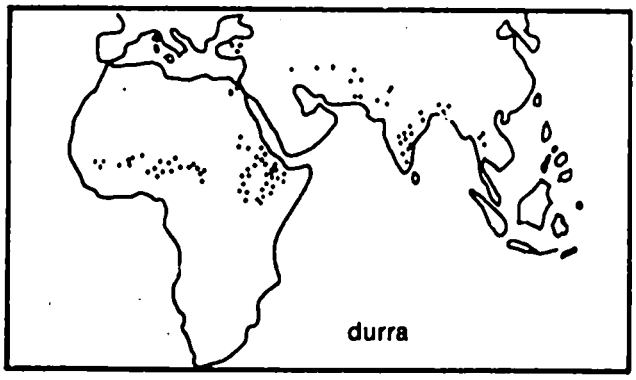


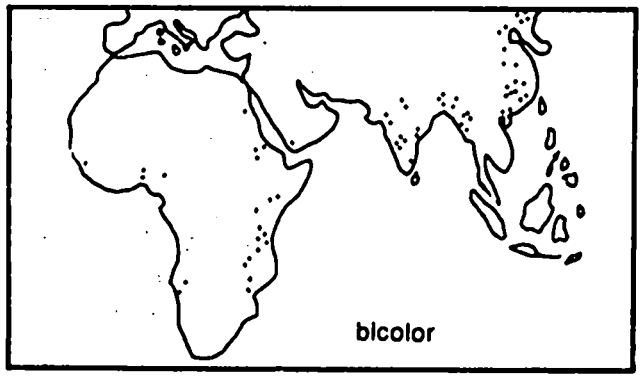


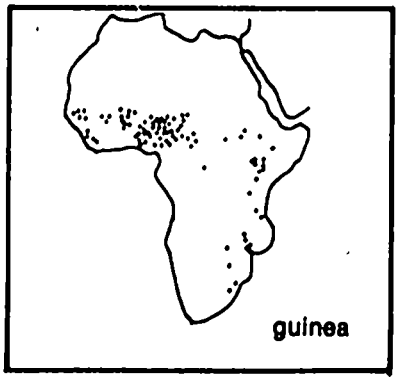


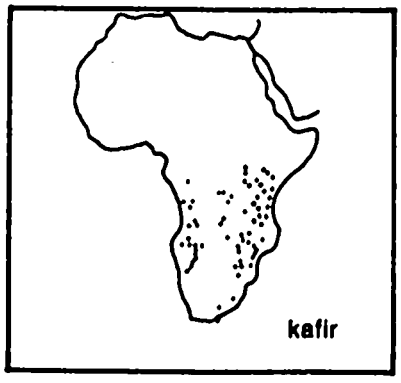


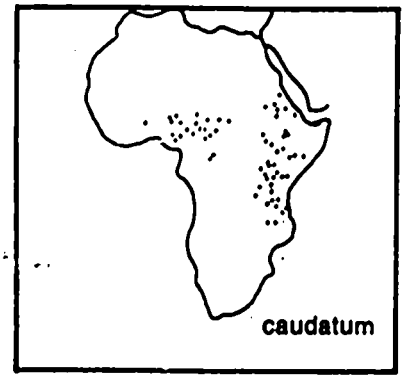
Cultivated:











sorghum from Africa and perennial taxa from S. Europe and Asia. The other sections contain only wild species. In section *Sorghum*, de Wet recognizes three species:

1. *S. halepense* (L.) Pers. (2n = 40), a rhizomatous (perennial) species, occurring from S. Eurasia east to India.
2. *S. propinquum* (Kunth) Hitchc. (2n = 20), rhizomatous, from S. India, Sri Lanka, and Burma eastwards to the southeast Asian islands.
3. *S. bicolor* (L.) Moench (2n = 20), all annual taxa as recognized by Snowden (1936, 1955), comprising a quite variable complex of cultivated sorghums: subsp. *bicolor*; a wild African complex, subsp. *drummondii* (Steud.) de Wet; and weedy introgressed derivatives, subsp. *arundinaceum* (Desv.) de Wet et Harlan.

De Wet's 1978 treatment lists 28 Snowden taxa in subsp. *bicolor*, 7 in subsp. *drummondii*, and 13 in subsp. *arundinaceum*. The numbers differ from those of Snowden's work because of regrouping and synonymy.

Murty et al. (1967) divided about 4000 entries in the World Sorghum Collection into eight subseries and 70 preliminary working groups. These working groups are more or less an extension of the classification made by Snowden and have been found convenient by some workers.

The collection was then classified by Murty (1972), using a number of different statistical procedures, which resulted in a division of the genus sorghum into nine groups: *S. roxburghi*, *S. conspicuum*, *S. arundinaceum*, *S. nervosum*, *S. durra*, *S. subglabrescens*, *S. sudanense*, *S. halapense*, and *S. virgatum*.

Cultivated Sorghum

Harlan and de Wet (1972) have developed a simplified, informal classification useful to plant breeders for the cultivated sorghums and their closest wild relatives. The cultivated taxa, covering 28 (out of 31) species of Snowden's series *Sativa* (de Wet 1978), are partitioned into the following races under *S. bicolor* subsp. *bicolor*:

Basic races:

1. Race bicolor (B)
2. Race guinea (G)
3. Race caudatum (C)
4. Race kafir (K)
5. Race durra (D)

Hybrid races:

6. Race guinea-bicolor (GB)
7. Race caudatum-bicolor (CB)
8. Race kafir-bicolor (KB)
9. Race durra-bicolor (DB)
10. Race guinea-caudatum(GC)
11. Race guinea-kafir (GK)
12. Race guinea-durra (GD)
13. Race kafir-caudatum(KC)
14. Race durra-caudatum(DC)
15. Race kafir-durra (KD)

The 15 races of cultivated sorghum can be identified by mature spikelets alone, although head type is sometimes helpful. The classification is based on five fundamental spikelet types described by Harlan and de Wet (1972):

Bicolor: Grain elongate, sometimes slightly obovate, nearly symmetrical dorso-ventrally; glumes clasping the grain, which may be completely covered or exposed as much as 1/4 of its length at the tip; spikelets persistent.

Guinea: Grain flattened dorso-ventrally, sub-lenticular in outline, twisting at maturity 90 degrees between gaping involute glumes that are nearly as long to longer than the grain.

Caudatum: Grain markedly asymmetrical, the side next to the lower glume flat or even somewhat concave, the opposite side rounded and bulging; the persistent style often at the tip of a beak pointing toward the lower glume; glumes 1/2 of the length of the grain or less.

Kafir: Grain approximately symmetrical, more or less spherical, not twisting, glumes clasping and variable in length.

Durra: Grain rounded obovate, wedge-shaped at the base and broadest slightly above the middle; the glumes very wide, the tip of a different texture from the base and often with a transverse crease across the middle.

Sketches of the basic spikelet are presented in Figure 1.1. Harlan and de Wet note that:

> The hybrid races are exactly what one would expect them to be. Races that are half guinea have grains

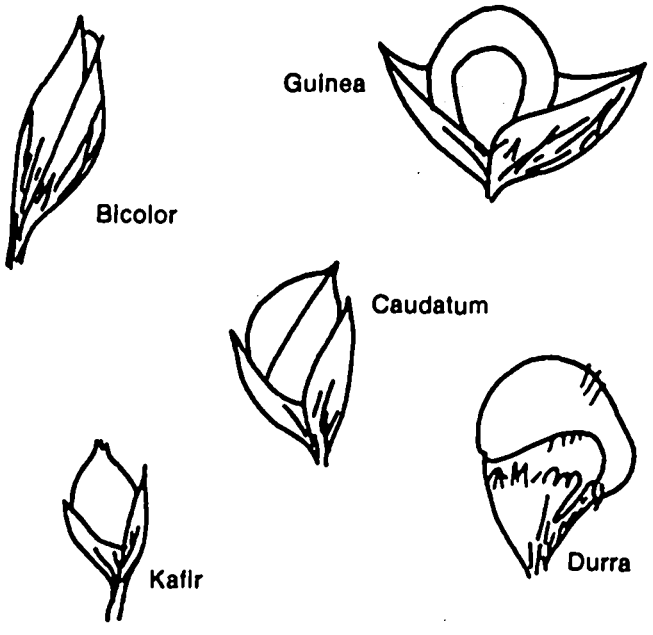


Figure 1.1: Classification of sorghum by basic spikelet type.

that twist somewhat, but not as completely as in the true guinea. Races that are half caudatum have grains that are turtle-backed, but not as extreme as in the true caudatums. Races that are half durra have grains broadly rounded above, but less conspicuously obovate than pure durra and the transverse crease may or may not be present. Races that are half kafir are appropriately modified in the direction of kafir and the half bicolor races are modified in the direction of bicolor.

Harlan (1972, p. 515) reports that:

In Africa, the distribution of indigenous materials is rather consistent. Guinea is primarily West African with a secondary center in Malawi-Tanzania. Caudatum is most abundant from east Nigeria to eastern Sudan and southward into Uganda. Kafir is primarily a race of East Africa, south of the equator and southern Africa. Durra is dominant in Ethiopia and westward across the continent in the driest zones of sorghum culture near the Sahara. The hybrid races are found rather consistently in the expected places; e.g., guinea-caudatum occurs where guinea and caudatum overlap (Nigeria, Chad, Sudan); durra-caudatum occurs in northern Nigeria and parts of Sudan where durras and caudatums are also found, etc.

The bicolor race occurs on a minor scale almost everywhere in Africa. The sweet types used for chewing are usually bicolors, and some are used for beer. They are seldom grown on a large scale. On the other hand, the highland Ethiopian sorghums belong to the durra-bicolor race and are grown very extensively. Bicolor races are frequently reconstituted locally through introgression between grain sorghums and wild and weedy sorts that are very abundant in central and eastern Africa.

Some of the hybrid races are unknown from indigenous collection, but show up in experiment station productions. In studying the Snowden collection at Kew, for example, I could find neither true kafir north of the equator nor true durra south of the equator and kafir-durra was missing. The Snowden collection has the advantage of being assembled about 40 years ago (early thirties) before material became so widely distributed.

Indian sorghums are mostly durra, guineas, and guinea-kafirs, with some bicolors grown on a minor scale. The American grain sorghums are now almost entirely kafir-caudatums. The Nigerian Kauras are durra-caudatums; the Zera zeras and Hegaris are caudatums. What is called Feterita in Sudan ranges from guinea-caudatum through caudatum to durra-caudatum. Broomcorns, sorgoc, and sudangrass fall under race bicolor.

Cultivated sorghums are more variable than the wild-weed complexes. However, it is possible to distinguish five more or less distinct cultivated complexes, each with an essentially recognized distribution:

S. bicolor subsp. *bicolor* race guinea: the commonly cultivated sorghum of West Africa, where rainfall is over 1000 mm annually. The morphological affinities and distribution indicate that the race guinea was probably derived from selection among wild members of the variety *arundinaceum*.

S. bicolor subsp. *bicolor* race kafir: the most commonly cultivated sorghum south of 5° N and east of 20° E. It is also cultivated from northern Nigeria west to northern Ghana, where there is a gene flow between the races guinea and kafir. There is no apparent center of origin for race kafir, probably due to migrations of the Bantu people. Their migrations since man's earliest history have brought all of the major cultivars into contact. This race appears to be of strictly African origin, and its distribution and morphological affinities suggest that it arose from variety *verticilliflorum*.

S. bicolor subsp. *bicolor* race durra: widely cultivated in Arabia and Asia Minor, and durra types are cultivated in India, Burma, along the Nile Valley, and in Ethiopia. There appear to be three centers of morphological diversity: the Ethiopian-Sudan region, the Near East, and India.

S. bicolor subsp. *bicolor* race bicolor: has its greatest diversity in Asia but is also widespread in Africa. Some cultivars are almost strictly African,

some are Asian, a few occur in Southeast Asia, and some are found on the South China coast. It appears that this race arose in East Africa from the variety *aethiopicum* and that the great diversity found in Asia occurred after its introduction there.

S. bicolor subsp. *bicolor* race caudatum: dominant in parts of Sudan, Chad, Nigeria, and most of Uganda. This is a very important race agronomically, especially in combination with other races.

Wild Sorghum

The weedy and wild relatives of the grain sorghums, earlier classified primarily in series *Spontanea* Snowden, are now listed in subsp. *drummondii* and subsp. *arundinaceum* (de Wet 1978). The wild relatives included in the classification of Harlan and de Wet (1972) as races *arundinaceum*, *aethiopicum*, *virgatum*, and *verticilliflorum* are now included in subsp. *arundinaceum*; and *propinquum* has been recognized as a separate species of the genus *Sorghum*. The distribution of the wild taxa, as adapted from de Wet el al. (1970) and de Wet (1978), is shown in Table 1.2, page 10.

The weedy taxa of subsp. *drummondii* are stable hybrids of the cultivated races and the wild taxa in *Sorghum bicolor*. These "species" have less tough racemes. The wild "species" have fragile racemes, and the plants usually inhabit natural grass vegetation but may invade cultivated fields.

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Table 1.2: Distribution of the wild taxa (adapted from de Wet et al. 1970, and de Wet 1978).

Subsp. *drummondii*	
S. atterimum Stapf	West tropical Africa, Sudan, Upper Nile region; spontaneous in fields.
S. drummondii (Steud.) Millsp. et Chase	West tropical Africa, now also in southern USA; spontaneous in cultivated lands.
S. elliotii Stapf	Uganda; weedy, around villages.
S. hewisonii (Piper) Longley	Sudan to Somalia; weedy, around villages and in cultivated fields.
S. nilotlcum (Stapf ex Piper) Snowden	Southern Sudan to eastern Zaire, and eastward to Kenya; along streambanks and weedy cultivated fields.
S. nitens (Busse et Pilger) Snowden	Tanzania, along the Bubu River.
S. sudanense (Piper) Stapf	Sudan to Egypt; along streambanks and weedy along irrigation channels.
Subsp. *arundinaceum*	
S. arundinaceum (Desv.) Stapf	Wet tropics along the Guinea coast, across Zaire to northern Angola; forest grass in low-lying areas and along streambanks.
S. aethiopicum (Hack.) Rupr. ex Stapf	Ethiopia, Sudan.
S. brevicarinatum Snowden	Northeastern Zaire, southward along the lakes to the Usugara district of Tanzania; along streambanks and irrigation ditches.
S. casteneum Hubb. et Snowden	Uganda; in low-lying wet areas
S. lanceolatum Stapf	Sudan, westward to northern Nigeria, and south to Uganda; in swampy areas or along streambanks.
S. macrochaeta Snowden	Southern Sudan to eastern Zaire; along streambanks and lake shores.
S. panicoides Stapf	Eastern Ethiopia; habitat not known.
S. pugonifolium Snowden	India: Punjab; this taxon is allied to *S. somaliense* and is likely a recent introduction from Africa.
S. somaliense Snowden	Somalia; water courses and damp areas.
S. usumbarense Snowden	Tanzania; humid habitats along rivers in Usambara district.
S. verticilliflorum (Steud.) Stapf	Kenya to South Africa; as roadside weeds in damp areas, along streambanks and irrigation ditches, or as weeds in cultivated fields.
S. virgatum (Hack.) Stapf	Sudan, northeastern Chad, Egypt; in dry regions along streambanks and irrigation ditches.
S. vogelianum (Piper) Stapf	Cameroon and Nigeria; tropical forest grass of river banks.

SECTION 2
THE SORGHUM PLANT

GROWTH STAGES AND MORPHOLOGY

Section 2 is a brief consideration of some of the anatomical and physiological aspects of the crop. Emphasis has been placed on those aspects that will be useful to breeders; for example, floral bud development, development of leaves, and the anatomy of the spikelet. The reader is also referred to the discussion of plant height and maturity in Section 3.

Growth Stages

Vegetative Phase

Germination and Seedling Development

When a seed is placed in moist soil it takes up water and swells. Germination occurs quickly and in warm soils (20° C or above) the coleoptile first appears above the ground after 3 or 4 days (longer, up to 10 days, in colder soils—13 to 20° C). As the seed swells the seed coat breaks, and a small coleoptile and primary root (radicle) emerge (Plate 2-9). The coleoptile grows longer and several more primary roots appear (Plate 2-10). The coleoptile begins to emerge from the ground, and the first leaf breaks through the tip (Plate 2-10). The young plant begins to grow, adding more leaves, and the coleoptile remains as a sheath at the base of the plant (Plate 2-11). The mesocotyl (Plate 2-11c) grows during this period, and a node is formed at the base of the coleoptile just below the ground line. Secondary roots begin to develop from this node when the plant is 3 to 7 days from emergence (Plate 2-11f). The young seedling is using food stored in the endosperm during this period. About the time the secondary roots have begun to develop, the mesocotyl begins to die and the major root system develops from secondary or adventitious roots.

Some sorghums tiller profusely, especially the sudangrasses and forage sorghums. The grain sorghums vary in their capacity to tiller, but usually do so only if there is adequate moisture or a poor stand. In normally tillering varieties, tillers develop from adventitious buds at the basal node soon after the secondary roots develop. Heads on the main stem flower at about same time as those on the tillers, or the heads on the tillers may flower later. The plant remains in a vegetative phase for about 30 to 40 days, during which all leaves are formed. After this period, growth occurs by cell elongation.

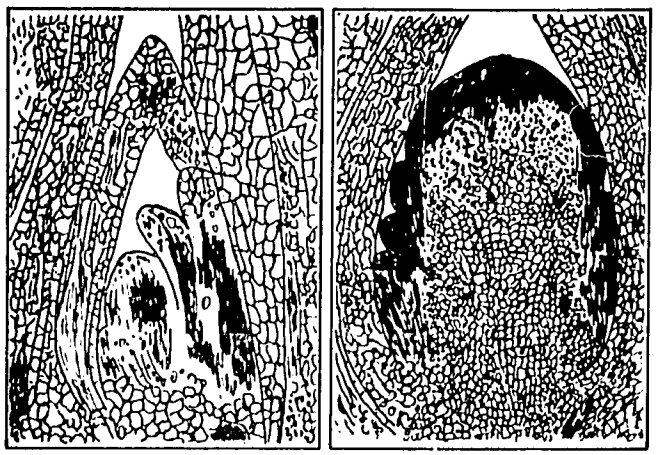
Reproductive Phase

Inflorescence Development and Fertilization

The floral initial forms (Plates 3 and 4-11) 30 to 40 days after germination (but floral initiation may range from 19 to 70 days or more) (Fig. 2.1). Usually, the floral initial is 15 to 30 cm above the ground when the plants are some 50 to 75 cm tall. Floral initiation marks the end of the vegetative growth due to meristematic activity. The grand period of growth in sorghum follows the formation of a floral bud and consists largely of cell enlargement.

During the period of rapid cell elongation, the floral initial develops into an inflorescence (Plate 3). About 6 to 10 days before flowering, the boot will form as a bulge in the sheath of the flag leaf. This will occur, in a variety that flowers in 60 to 65 days, about 55 days from germination. Sorghum usually flowers in 55 to 70 days in warm climates, but flowering may range from 30 to more than 100 days.

The sorghum head begins to flower at its tip and flowers successively downward over a 4- or 5-day period. Because all heads in a field do not flower at the same time, pollen is usually available for a period of 10 to 15 days. At the time of flowering, the glumes open and the three anthers fall free, while



Vegetative bud Floral bud

Figure 2.1: Vegetative and floral buds.

the two stigmas protrude, each on a stif' style (Plates 4-2 and 4-6). Flowering frequently oc curs just before or just after sunrise, but may be delayed on cloudy damp mornings. The anthers dehisce when they are dry (but not in heavy dew or rain) and pollen blows into the air. Sorghum is primarily self-pollinated (about 2 to 10% or more cross-pollination); that is, the pollen from a head fertilizes most of the eggs on the same head. The pollen drifts to the stigma, where it germinates; the pollen tube, with two nuclei, grows down the style, to fertilize the egg and form a 2n nucleus and 3n endosperm,("n": see page 28, col.2, 4th para.). Sorghum has a 20-chromosome complement. The glumes close shortly after pollination, though the empty anthers and stigmas still protrude (except in the long-glumed types). The florets of some of the very long-glumed types do not open for fertilization—a phenomenon known as *cleistogamy*.

Cytoplasmic male sterility has been found in sorghum and has made possible the development of a hybrid seed industry. A good male-sterile plant will not develop anthers, but in some instances dark-colored shrivelled anthers with no viable pollen will appear. Partially fertile heads are also observed, and although the anthers frequently have viable pollen, the quantity is less than in normal plants. Viability of pollen in partially fertile plants is an important problem for seed producers.

Maturation Phase

Seed Development

The ovule begins to develop as a light green, almost cream-colored sphere; after about 10 days it begins to take size and becomes a darker green. It takes about 30 days for the seeds to reach maximum dry weight (physiological maturity). During this development, the seed passes through three stages: (1) "milk," (2) "early dough," and (3) "late dough." These terms, while commonly used, are not specifically defined. The seeds begin to turn from green to the color that they will be at maturity. The seeds contain about 30% moisture at physiological maturity; they dry to about 10 to 15% moisture during the following 20 to 25 days. During this period, they lose up to 10% of dry weight. The seed is ready for harvest at any time from physiological maturity to seed dryness; however, seed with more than 12% moisture must be dried before storage. It is easy to recognize the pericarp, the endosperm, and the embryo in a sliced mature dry seed (Plates 2-7 and 2-8).

Lower leaves begin to die and dry up during this period. By the time the grain begins to dry, four or five of the lower leaves may dry up and drop from the plant. There is a distinct varietal difference in the rate of senescence of remaining leaves. All leaves may be dried, or almost dried, at grain maturity; or the plant may remain green.

Morphology of Sorghum

Roots

The root system of sorghum is extensive, and there are many root hairs (almost twice that of maize, for example). An embryonic or primary root first appears upon germination (Plate 2-9). Several such roots develop (Plate 2-10); these are not branched or are sparsely branched (Plate 2-10). Secondary roots develop from the first node; it is these roots that develop into the extensive root system of the plant (Plate 2-11f). The primary roots subsequently die. Brace roots may appear later on the lowermost nodes and may be numerous if the plant is unadapted (Plate 5-9). These roots are not effective in uptake of water and nutrients.

The cultivated sorghums are either nonrhizomatous or very weakly rhizomatous, and are annual or (weakly) perennial. The root system, however, survives to support the development of ratoon crops (a second, third, or more growth of culms from the same root system) from adventitious buds at the base of the parent stem. Well-developed rhizomes are found only in the subspecies *halepense* (Johnson grass).

Culms

The culm, or stem, is made up of a series of alternating nodes and internodes. The stem is slender to very stout, measuring 0.5 to 5 cm in diameter near the base, becoming narrower at the upper end, and varying in length from 0.5 to 4m. It is solid, with a hard cortex or rind and a softer pith. Vascular bundles are scattered throughout the stem, but there are more near the peripheral area, where they are so closely associated that they form almost a solid ring. The vascular bundles in the central portion of the stem are larger than those at the periphery. The central bundles branch into leaf midribs, while the peripheral bundles branch to form the smaller veins in the leaf blade.

The pith may be sweet or insipid, juicy or dry. In older stems the pith may crack, especially if dry.

The node appears as a ring at the base of the leaf sheath; this is the point at which the leaf is attached to the stem (also the point at which brace roots develop). There is a complex anastomosis of vascular bundles from the stem to the leaf at this point (Plates 4-9 and 4-11). A bud forms at each node, except at the node to which the flag leaf is attached (Plate 4-9). These buds, at successive nodes, arise on alternating sides of the stem. At times these buds will develop to form axillary tillers (Plate 4-8). Basal tillers (Plate 4-10), if any, form at the first node.

Leaves

Leaves are variously distributed along the stem in sorghum; in some types they may be concentrated near the base, while in others they are more or less uniformly distributed. Leaves are borne at different angles to the stem, varying from almost vertical to near-horizontal. The leaf blade may be straight, or may slowly loop over, forming an arc. The tip of the leaf may even drop down. The leaves vary in length, usually being shorter and smaller at the top (the top leaf is called the flag leaf); in the lower mid section, they may be as long or slightly longer than those at the base of the plant. Leaves may be as long as 1 m and may vary in width from 10 to 15 cm. The plants vary greatly in number of leaves: in well-adapted plants there are usually 14 to 17 leaves, but less adapted plants may have as many as 30 leaves.

Generally, the embryo in the seed will have five to seven embryonic leaves, the greater number being found in the more mature seeds. Table 2.1 is taken from work done at the Texas Agricultural Experiment Station, Chillicothe, Texas, USA. This table shows that 3 to 6 days elapse between the differentiation of successive leaves, with some varieties producing leaves faster than others.

A sorghum seed reaches physiological maturity in about 30 days and at this time has six or seven

Table 2.1: Time required to lay down a leaf in the vegetative bud (meristem) of sorghum (assuming seven leaves in the embryo).

Cultivar	Number of days to head initiation	Total no. of leaves	Number of leaves produced after germination	Days per leaf
Sooner Milo	32	13	6	5
Texas Milo	39	18	11	4
Hegari	48	18	11	4
Kalo	39	17	10	4
Calif.W. Durra	34	14	7	5
Spur Feterita	36	19	12	3
Freed	32	12	5	6
Manko	47	17	10	5
Bishop	39	17	10	4
Sumac	39	16	9	4
Black Hull Kafir	39	16	9	4
Jap. D. Broomcorn	39	15	8	5

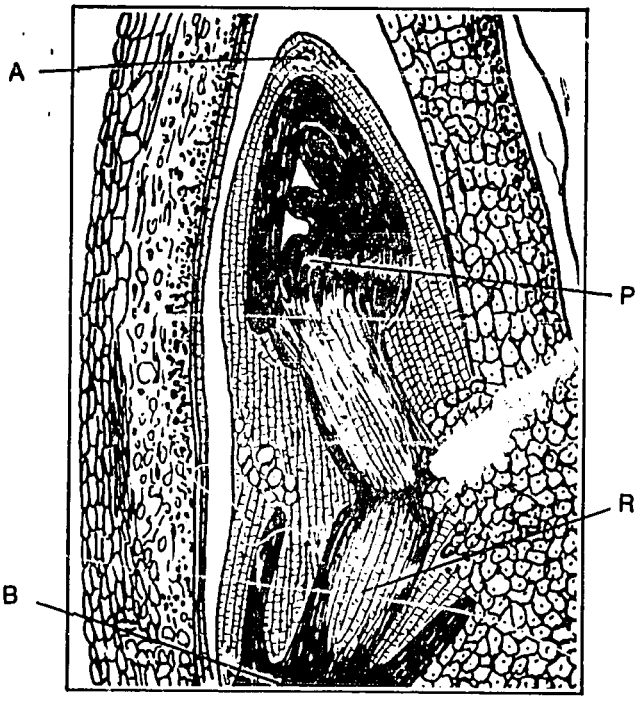


Figure 2.2: Longitudinal section of embryo 16 days after pollination: (A) coleoptile, (B) coleorhiza, (P) plumule, (R) radicle.

embryonic leaves. Approximately the same amount of time (4 to 5 days) is required to lay down a leaf in the embryo as in the vegetative growing point, the meristem (Table 2.1).

The leaves are borne alternately in two ranks along the stem, and consist primarily of a sheath and a blade. The sheath is attached to a node and surrounds the internode, and frequently the node above it, before the blade extends outwards. Frequently, the sheaths attached to lower nodes will cover the nodes above, but those higher on the plant will not extend as far as the node above. This sheath is frequently covered with a waxy bloom; at times the bloom is quite pronounced (Plate 5-1). The blades are broad at the base and taper upward to a fine point; they are glabrous, except on the inside just above the ligule and on the outside near the junction with the sheath. The margins of the leaf are smooth or scabrid, especially on the upper half. The midrib is prominent, greenish or white, flattened or slightly concave on the upper surface and convex on the lower one. The blades are thicker at the base than at the tip and along the midrib than along the margins. When damaged, the injured spot will turn tan, red, or deep purple (almost black), depending on the plant color.

There is a short (1 to 3 mm) membranous ligule at the junction of the leaf blade with the sheath (Fig. 2.3).

Leaves of the wild species are frequently long (30 to 75 cm) and slender (0.5 to 7 cm in width).

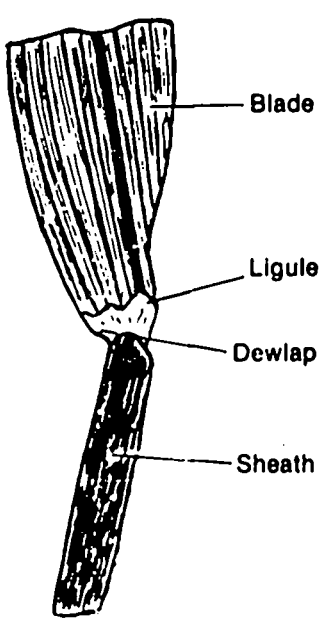


Figure 2.3: Sorghum leaf.

Inflorescence

Panicle

The panicle may be short and compact or loose and open: 4 to 25 cm or more long, and 2 to 20 cm or more wide. The central axis of the panicle, the rachis, may be completely hidden by the density of the panicle branches or completely exposed. The rachis differs greatly in its shape and length—from long and thin to short and stubby. The rachis may be striated (frequently channeled), and it may be hairy or glabrous. Several branches are borne at each node, and these branches vary in length, may be stout or slender, rigid or flexible, hairy or almost glabrous, branched beginning near the base or not branched until near the tip. The panicle usually grows erect at the apex of the culm, but may be recurved.

The wild and weedy sorghums have a rather loose panicle with spreading branches. The panicle is often large and pyramidal in shape.

Raceme

The raceme always consists of one or several spikelets. One spikelet is always sessile and the other pedicellate (Plate 4-5), except the terminal sessile spikelet, which is accompanied by two pediceled spikelets. The racemes vary in length according to the number of nodes and the length of the internodes. There are 1 to 4 nodes in some species, and 5 to 8 nodes in others; internodes vary in length, thickness, and hairiness, depending on the species. On the pediceled spikelets, the pedicels vary in length from 0.5 to 3.0 mm, and usually are very similar to the internodes.

Sessile Spikelets: The sessile spikelet varies in shape from lanceolate to almost rotund and ovate (Fig. 2.4) and is sometimes depressed in the middle. The color is green at flowering, changing to shades of straw, cream, buff, yellow, red, brown, purple, or almost black at grain maturity. The intensity and extent of coloring on the glumes is variable. Glumes vary from quite hairy to almost hairless (Plate 4-5). The glumes are hard and tough in most species with the nerves frequently obscure except near the tip (Plate 4-5). Some species have thin and brittle glumes, while others have thin and papery ones. The lower glume is usually somewhat flattened and conforms more or less to the shape of the spikelet, while the upper one is more convex or boat shaped. The seed may be enclosed by the glume or may protrude from it, being just visible to almost completely exposed.

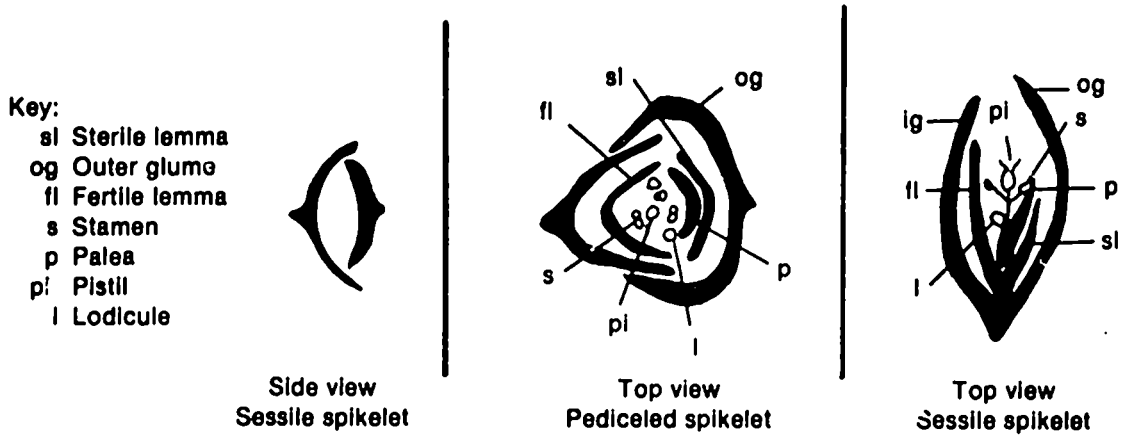


Figure 2.4: Components of the pediceled and sessile spikelets. The sterile or pediceled spikelet is represented by the empty glumes. (Source: Progress Report No. 5, Sorghum Physiology Program, University of Nebraska, USA.)

There are two lemmas, each a delicate white tissue easily overlooked on a casual glance. The lower lemma is elliptic or oblong, about equal in length to the glume (Plate 2-3); the upper lemma is shorter, more ovate, and may be awned. There are also two lodicules and a palea, but these are much reduced and are of little interest. Sorghum has two pistils and three stamens. (Plate 4-6). Each fluffy stigma is attached to a short stout style extending to the ovary (Plates 4-2 and 8-4). The anthers are attached to long threadlike filaments (Plate 4-2).

Seed or Caryopsis: Seeds are more or less spherical in shape, varying to somewhat flattened on one side (turtle-backed). They range tremendously in pericarp color (red, brown, white, yellow, cream) and have either a dull or pearly luster. The testa may also be colored, usually a dark red to dark brown. The endosperm is usually white, though it may be yellow. Yellow endosperm color is due to carotenoid pigments that have a relatively low vitamin A activity. There often are two fairly distinct lines extending from the apex to the base of the seed. The embryo mark (scutellum) varies in length from about one-half to two-thirds the length of the grain, and is elliptic to elliptic oblong, concave to flat, or (rarely) convex (Plate 2-4). The hilum is at the base on the side opposite the embryo. The hilum frequently turns dark at about the time the seed reaches physiological maturity. The endosperm varies from soft with little corneous portion to a solid corneous seed condition. Seed size varies from very small (less than 1 g/100 seeds) to large (5 to 6 g/100 seeds) (Plate 4-7).

Pediceled Spikelets: These are much narrower than the sessile spikelets, usually lanceolate in shape. They may be smaller, the same size, or longer than the sessile spikelets (Plate 4-5). They are male or neuter in sex, but (very rarely) may have a rudimentary ovary. The lemmas are much reduced in size and only rarely does the upper lemma have an awn.

PLATE 2. THE SORGHUM PLANT

(Numbers 1, 5, and 6 were deleted from this plate as not relevant to this volume—Ed.)

2-2. A mature floret—seed and glumes

2-3. Parts of the sorghum floret:
a - lower glume
b - lower lemma
c - upper glume
d - upper lemma (lying in glume) with awn attached
e - seed situated between the upper and lower lemmas

2-4. Sorghum seed (*caryopsis*):
a - The embryo is apparent in this seed.
b - The black hilum is apparent at the base of the seed. There is an indication that when this hilum turns dark, the seed has reached physiological maturity; black layer formation can be used as an indicator of physiological maturity (maximum dry weight).

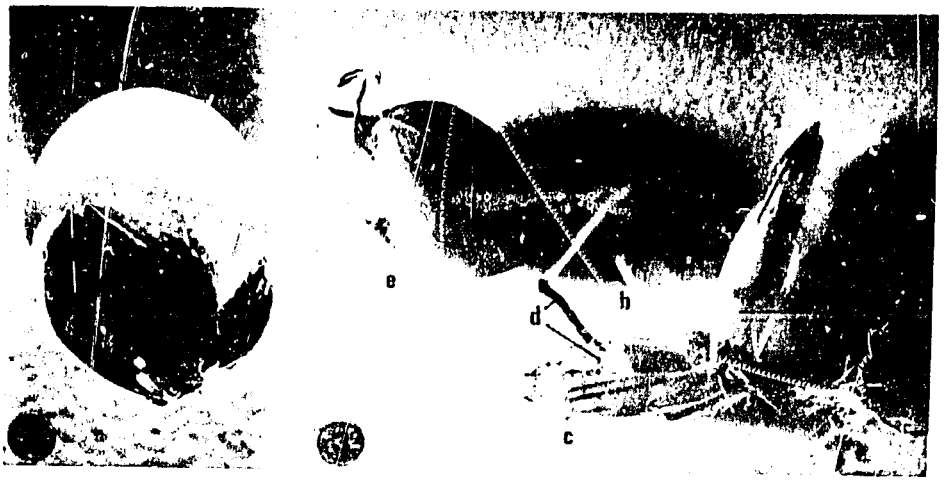
2-7. A longitudinal section of a sorghum seed showing:
a - the pericarp
b - the endosperm
c - the embryo

2-8. A cross section of a sorghum seed showing:
a - the pericarp
b - the endosperm
c - the embryo

2-9. A germinated sorghum seed showing:
a - the coleoptile
b - the primary root
c - the seed

2-10. Stages of development:
a - tip of primary leaf
b - the coleoptile
c - the seed
d - primary roots

2-11. Stages of development:
a - leaves
b - end of coleoptile
c - mesocotyl
d - seed
e - primary roots
f - secondary or lateral roots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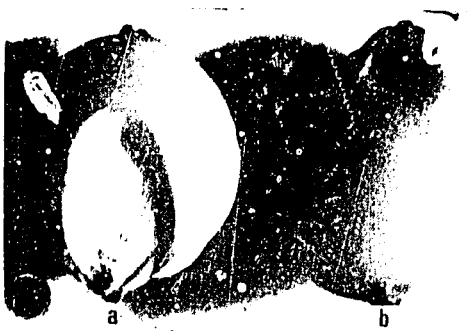
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PLATE 3. DEVELOPMENT OF THE SORGHUM HEAD

3-1. Leaf primordium (LP) and vegetative shoot apex (a) of sorghum.

3-2, 3-3. Beginning of the elongation of the apical meristem before floral development.

3-4, 3-5. Differentiation of the primary branch primordia (bp1) on the floral apex.

3-6. Floral development showing primary branch primordia over the entire apex.

3-7. Differentiation of secondary branch primordia (bp2) on the primary branch primordia.

3-8. Panicle showing well-developed secondary branch primordia.

3-9. Panicle branch showing secondary and tertiary branch primordia.

3-10. Panicle beginning to elongate, panicle branch development easily visible.

3-11. Panicle branch.

3-12. Mature panicle branch showing the fertile (sessile) spikelet (fs) and the sterile (pediceled) spikelet (ss).

3-13. Spikelet development showing the inner glume (ig) and outer glume (og) primordia.

3-14. Stamen primordia (st) can be observed as three spots shining in the illuminating light.

3-15. Primordia of the fertile (sessile) spikelet (fs) and the sterile (pediceled) spikelet (ss).

3-16. Outer glume (og), inner glume (ig), and sterile (lower) lemma (sl).

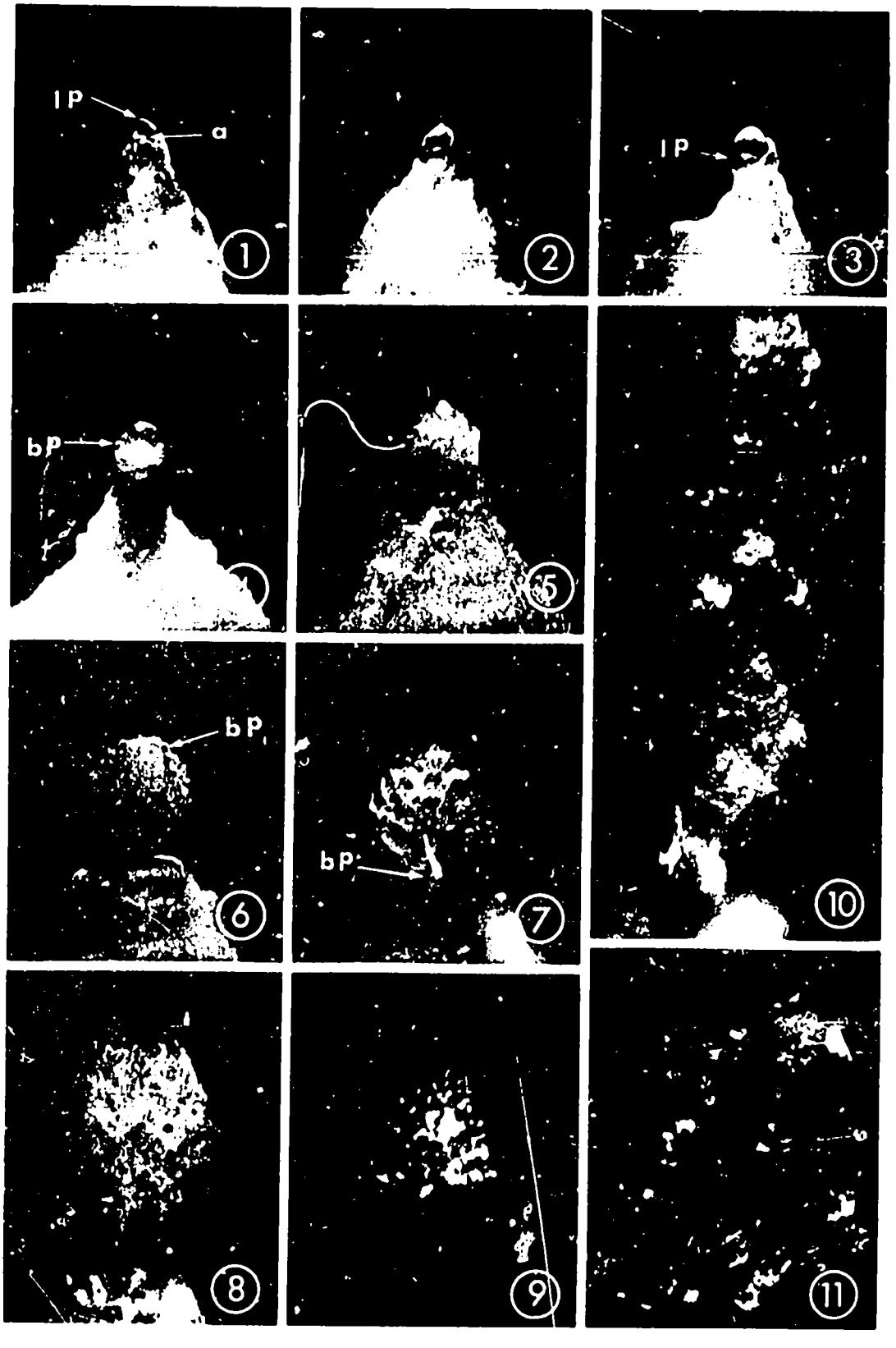
3-17. Upper (l) and lower (sterile—sl) lemma, stamen (st), and pistil (pi) development.

3-18. Floret parts: outer glume (og), inner glume (ig), sterile lemma (st), upper lemma (l), receptacle (r), palea (p), lodicules (lo), stamens (st), and pistil (pi).

3-19,3-20. Panicle branch from two stages of development: U = upper, M = middle, and B = lower portions of the inflorescence.

3-21. A fully developed panicle.

(Photographs courtesy of R.C. Lommasson and K.W. Lee, Department of Botany; and J.D. Eastin, Department of Agronomy, University of Nebraska, Lincoln, Nebraska.)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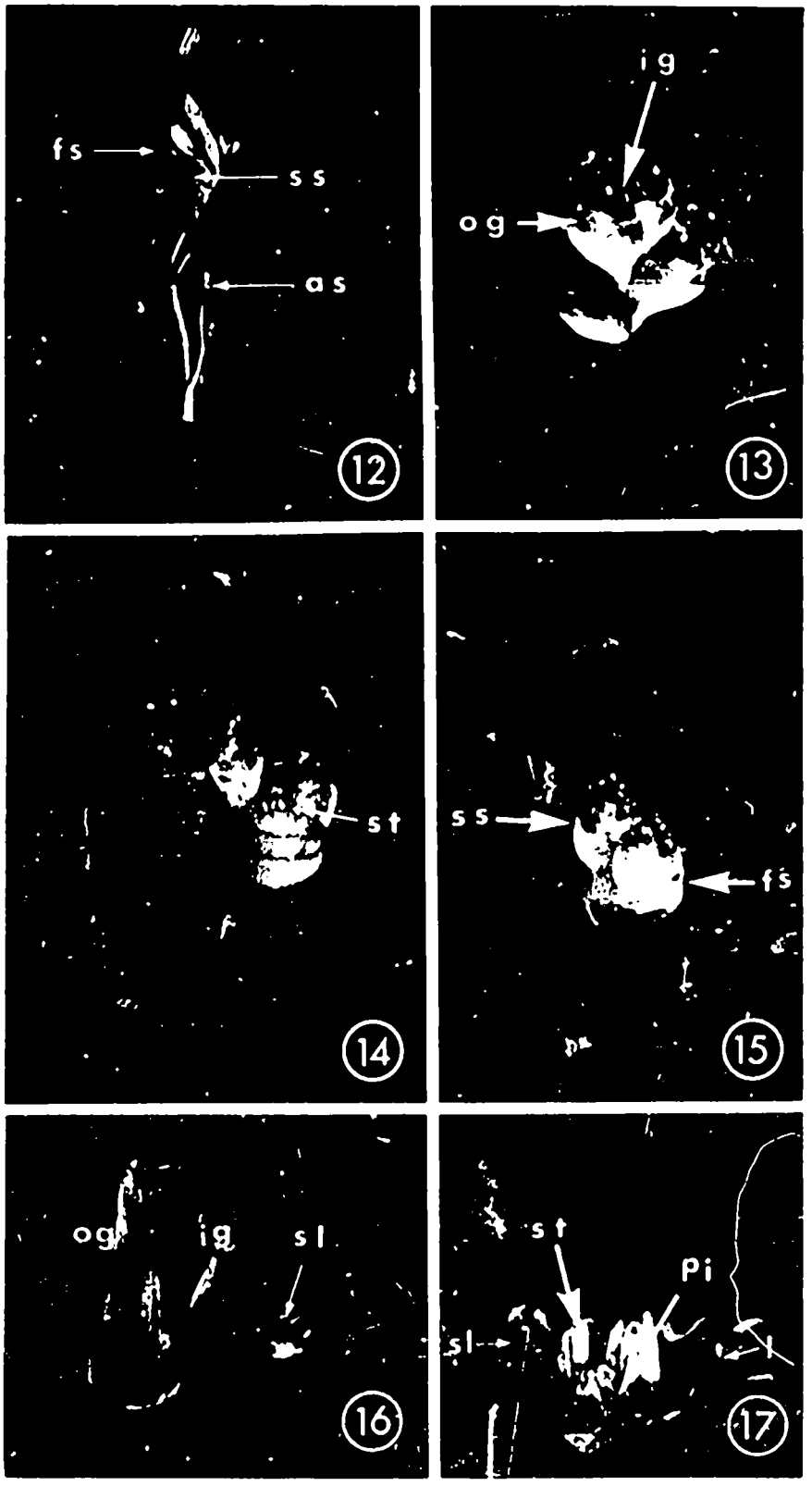
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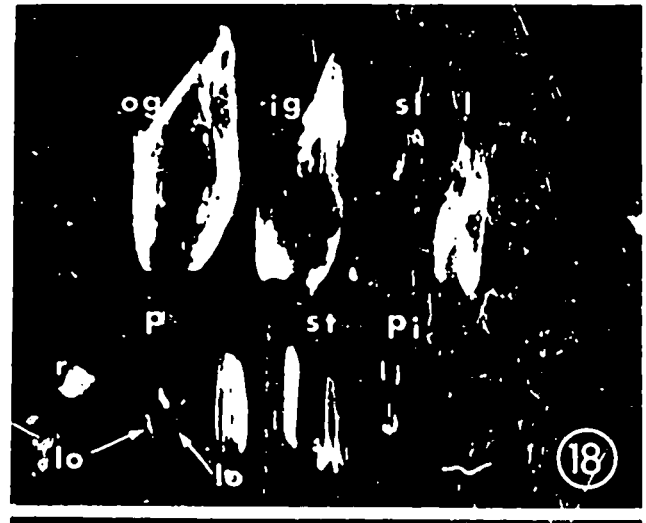
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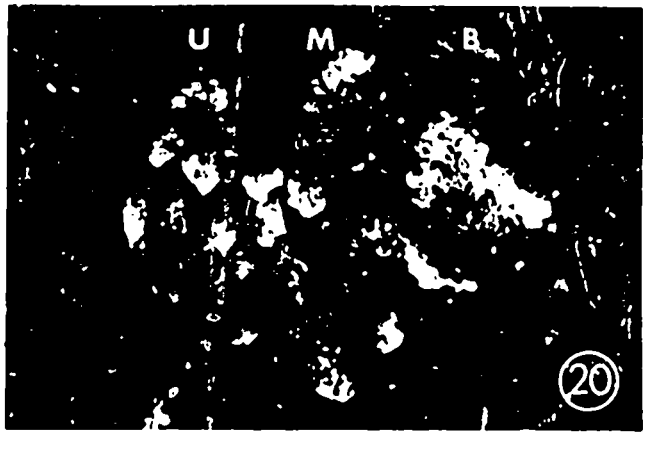
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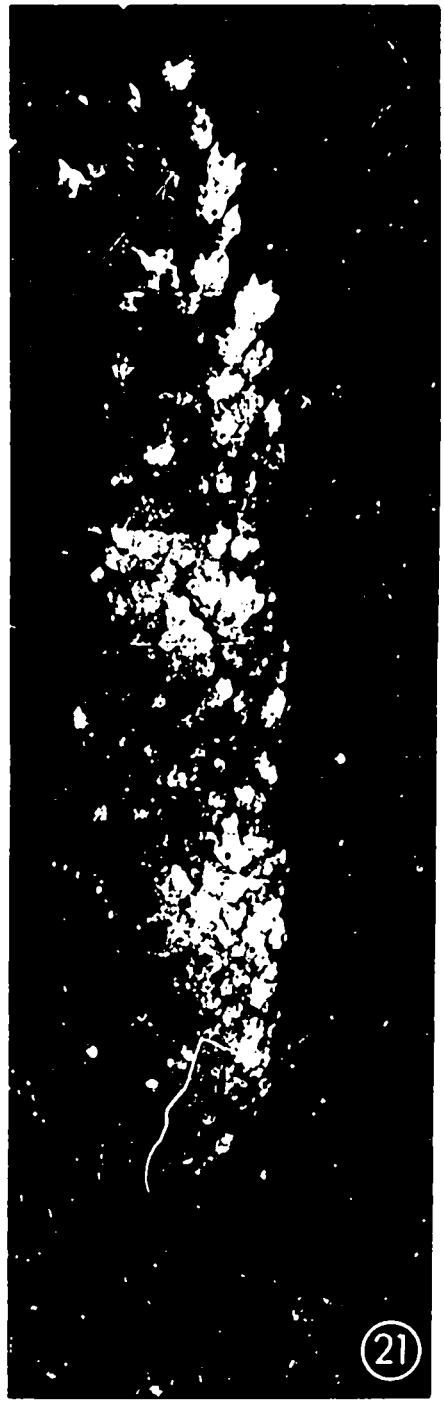
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PLATE 4. THE SORGHUM PLANT

4-1. A vigorous F_1 hybrid. The plant is well adapted showing good head size and good exsertion of the head from the flag leaf.

4-2, 4-3. The head in flower. Flowering begins at the top and proceeds downward, requiring 4 to 5 days for the whole head to flower (3). The fluffy stigmas and anthers of a portion of the head in flower are shown in photograph 2.

4-4. A panicle branch showing secondary and tertiary branching.

4-5. The tip of the tertiary branch showing sessile and pediceled spikelets. There are two pediceled spikelets in association with the terminal floret and one with subterminal ones:
a - sessile spikelets
b - pediceled spikelets with terminal florets
c - pediceled spikelets with subterminal florets
d - pedicel
e - top of panicle branch
f - panicle branch

4-6. The floret in flower; note the two fluffy stigmas and the three anthers.

4-7. Seed size in sorghum. The middle row of seeds is from combine kafir 60, an average seed size for the crop. The larger seeds are of a Sudanese variety, Mugud.

4-8. Axillary branches; some varieties are more prone than others to develop such branches, especially if the main head is destroyed.

4-9. An axillary bud in sorghum. (A small piece of black paper has been placed under the bud to enhance contrast.)

4-10. Tillers arising from the crown.

4-11. The rudimentary panicle showing two stages of early development.

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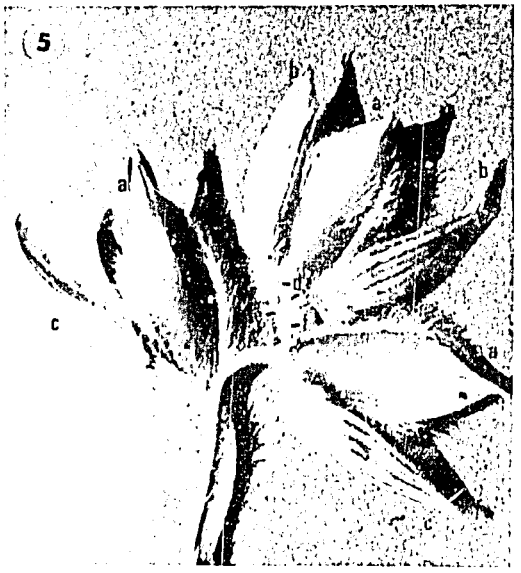
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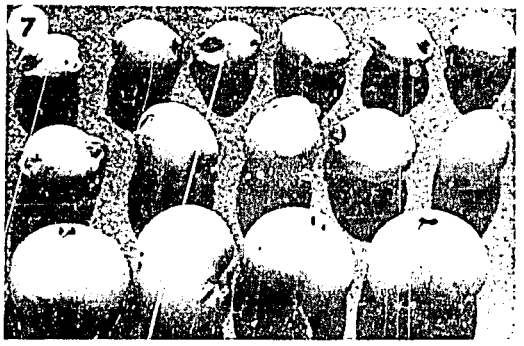
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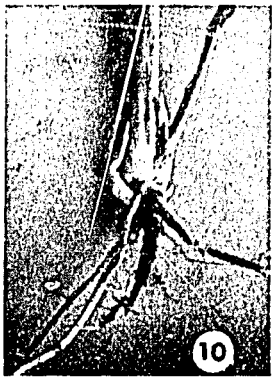
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PLATE 5. SOME MORPHOLOGICAL AND PHYSIOLOGICAL CONSIDERATIONS

5-1. Sorghum has a waxy bloom on stem and leaves. This bloom may be quite pronounced on some varieties. It can be easily rubbed from the plant and usually wipes onto one's clothing in the field.

5-2. Complete sterility. Occasionally, on male-sterile plants, the upper portion of the head will become white and be both male and female-sterile. The reason for this is not known. This problem may occur once in an area (even on a particular field) and not occur again for a long time.

5-3, 5-4. Anthers from normal (4 on left), semi-sterile (4 in center), and male-sterile (2 on right) plants. Pollen from semi-sterile plants is apt to be fertile. Anthers on male-sterile plants, if shriveled and dark colored, will not shed any viable pollen. Photograph 4 was taken with light directed through (from below) the anthers.

5-5. Plants growing in a cool climate during a short day period. This variety growing in these conditions will flower when the plants are very small and the leaf number few. (Several plants in the foreground are in the boot leaf stage, while one in the background is in flower.)

5-6. Seedling vigor. This is an important characteristic of sorghum. A score can be developed, for example 1 to 5, to enable the breeder to take notes on this character.

5-7. Physiological deterioration of the leaves. The spots are the same as the plant color and the leaves are chlorotic. It is suspected in this case that this problem may be due to a soil condition.

5-8. Photoperiod problem. The plants in the foreground have made seed, while the tall rank ones in the background are still vegetative. Examination revealed that the growing point was very near the top of the plant. Photoperiod-sensitive plants will do this if planted during March or April at 10° latitude, mid-January to May at 18° latitude, and during the summer growing season at 35-40° latitude.

5-9. Rank, unadapted plants, as shown in photograph 8 usually have big broad leaves, a high leaf number, thick stems, and at times a proliferation of "brace" roots, as shown here.

5-10. Lodging, a very important negative characteristic commercially. Lodging notes should be taken by the plant breeder. The amount of lodging can be estimated, and categories such as 0-5, 5-10, 10-25, 25-50, 50-75, 75-90, 90-95, 95-100 are suggested. It is easier to see 0 to 5% lodging than 50 to 55%, hence the development of such categories.

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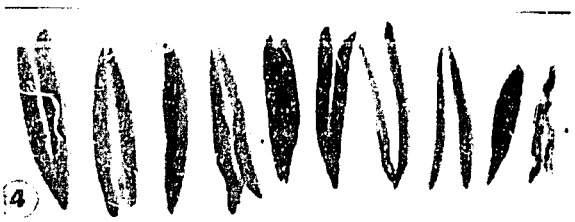
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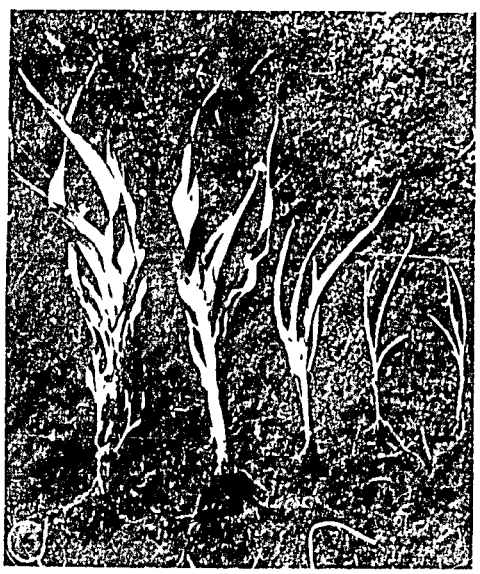
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SECTION 3
GENETICS

Plant breeding principles stem from the basic science of genetics. Thus a working knowledge of this science is necessary for a good understanding of breeding procedures. This section presents a general review and survey of genetic concepts of most importance to the plant breeder, including discussions of Mendelian inheritance and factors that change gene frequencies. The evolutionary forces in nature that change gene frequency (i.e., selection, migration, and mutation) usually operate over a long span of time. The plant breeder uses these same forces, in a controlled fashion, to change frequencies in a chosen direction and relatively quickly.

Section 3 describes many of the concepts that are put to use by the breeder in his practical sorghum improvement work. Mitosis and meiosis are described first, leading to a discussion of Mendelian genetics. Single-factor inheritance is outlined, followed by a brief review of the inheritance of quantitative traits. Gene frequencies and the forces that change these frequencies are treated next, with a concluding discussion of the genetics of sorghum.

These concepts are not easily grasped, but if understood they will serve the reader well in many aspects of plant breeding. Thus special study is encouraged, perhaps with additional reading in the references cited.

The first portion of Section 3, on Mendelian genetics, was written by Geoff Hawtin and revised by J.P. Moss, and the following portions, on quantitative and population genetics, were written by L.R. House.

Basic Genetics

Biological Variation

Biological variation is the basis of evolution, and plant breeders use this variation to direct and control evolutionary processes in developing new varieties. The breeder bases his observations and selections on measurements of the phenotype.

The *phenotype* of an organism can be defined as its observable properties—characters such as plant height, number of leaves, color of flowers, shape of anthers, growth rate, etc.

An individual plant derives its phenotype from two factors:

- the *genotype*, which is the genetic makeup of the plant; and
- the *environment*, which modifies the expression of the genotype.

Almost all of the characters that combine to form the phenotype of a plant are subject to some degree of variation, however slight, resulting from variation in either the genotype or the environment or both. Such variations in a plant's observable properties are called *phenotypic variations*. Variation due to differences in genotype is called *genetic variation*, and that due to the environment is called *environmental variation*.

The degree of variation in a particular character can be measured by means of a statistic called the *variance* (the square of the standard deviation). The phenotypic variance (V_P) is the sum of the genetic variance (V_G) and the environmental variance (V_E). Thus: $V_P = V_G + V_E$.

If plants having identical genotypes are grown in

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several different environments, the observed variation in the phenotype of a particular character will be entirely due to the effects of the environment. In this situation, $V_G = 0$ (zero) and $V_P = V_E$.

If, on the other hand, plants with different genotypes are grown in the same environment, the observed phenotypic variation will be due entirely to genetic differences between the plants. In this situation $V_E = 0$ and $V_P = V_G$. It is, of course, practically impossible to grow plants in identical environments: environmental variation can rarely, if ever, be eliminated completely.

The plant breeder, in attempting to develop improved varieties, bases his observations and selections on measurements of the phenotype. The genetic variation, however, is of most value to the breeder, since this is the hereditary portion of the total variation. He seeks to reduce, to control, or to accurately describe the environmental variation, so that the selections based on superior phenotypes will, in fact, be genetically superior.

Since heritable variation is of prime concern to the breeder, most of the following discussion focuses on this aspect of phenotypic variation.

The Basis of Heredity

Heredity is the process through which characteristics of parents are transmitted to their offspring. It has been shown that the expression of a character in an organism is highly dependent on the *genotype* (the genetic makeup) of that organism, though its expression may be modified by the effects of the environment.

If parents with identical genotypes are crossed, however, the genotype of the offspring will be composed of parts of the genotypes of both parents. So the genotype of the progeny may be the same as or different from the parents', and the resulting phenotype of the progeny may resemble one parent, both parents, or neither.

The science of *genetics* studies the degree of similarity or difference between an offspring and its parents. It attempts to explain how such similarities or differences are transmitted from generation to generation.

The genetic, or hereditary, information of an organism is contained in *genes*. Genes can be thought of as very small chemical factors that control the physiological process of the organism, and thus its structural development. A single gene may control a single character or several characters, or it may act in combination with other genes.

Genes are located on *chromosomes*, which are rod- or thread-shaped bodies within the cell nucleus. Each species has a characteristic number of chromosomes, and each specific gene is found on a specific chromosome and at a specific location (referred to as a *locus*) on that chromosome.

A gene can exist in different forms, which confer different characters on the plant. One form of a gene may confer genetic male sterility, the other confer fertility. Alternative forms of a gene at a given locus are referred to as *alleles*.

There are two identical sets of chromosomes (each set is known as a *genome*) in the nucleus of each cell: one set is derived from the male parent and the other from the female parent. A pair of corresponding chromosomes is called *homologous* chromosomes. A gene consists of an allele at a particular locus on a chromosome derived from the male parent and a corresponding allele at the same locus on the homologous chromosome derived from the female parent. If these two alleles are the same (for example, if both alleles confer male sterility in sorghum), then the phenotype of the plant is determined by their effect—the plants in the progeny will be male-sterile, and the plants are said to be *homozygous* for that character. If the two alleles are different, then the phenotype may be intermediate or one allele may dominate over the other. If the two alleles are different, the plant is said to be *heterozygous* for that gene.

The number of chromosomes in the *gamete* (pollen or egg cell) of a given species is known as the *haploid* number and is generally indicated by the letter n (in sorghum, n = 10). The normal number of chromosomes in a plant is 2n, and this is referred to as the *diploid* number. Thus, in the nuclei of sorghum cells, there are 2n, or 20, chromosomes.

The descriptions that follow are designed to provide a clearer idea of how, during plant growth, the number of cells increases by mitosis, and how gametes containing haploid cells are produced by meiosis. These descriptions provide a basis for discussion of the ways in which certain traits are inherited:

In the formation of the pollen and the ovule, a process occurs that is known as reduction division, or *meiosis*. In meiosis, cells with n chromosomes are produced from a cell with 2n chromosomes. Thus, during most of the life cycle of the plant, each cell nucleus has the diploid number of chromosomes (2n), except for the ovule and the pollen, which have the haploid number (n). When fertilization occurs, the n chromosomes from the pollen combine with the n chromosomes from the ovule to

produce a cell (the *zygote*) having the diploid number (2n) again. Division known as *mitosis* occurs in the formation of new cells from the zygote, and throughout the development of the mature plant. In mitosis the 2n chromosomes duplicate themselves exactly in the new cell.

In some plants more than the diploid number of chromosomes may be found; these are referred to as *polyploids*, (see p.47 ff.).

Mitosis

Plant growth is the result of two processes:

- an increase in cell number, and
- an increase in cell size.

Most active division of cells takes place in tissue, called *meristematic* tissue, that is located mainly at the apices of organs—for example, root tips. Two interrelated processes are involved in cell division:

- *mitosis*, the division of the nucleus to form two nuclei, each having the same number of chromosomes as, and identical genotype to, the parent cell, and
- *cytokinesis*, which is the division of the rest of the cell.

The process of mitosis occurs in a definite sequence of events, shown in Figure 3.1.

Process of Mitosis

Interphase:

This is the stage between divisions of the nucleus during which the chromosomes duplicate themselves in readiness for the separation that occurs during mitosis.

Prophase:

At the beginning of prophase, the chromosomes appear as long threadlike structures, but as prophase progresses they become coiled, shortened, and more distinct. Towards the end of prophase, the chromosomes appear to be solid and oval or rod-shaped, and by late prophase the chromosome can often be seen to have divided lengthwise into two separate units, called *chromatids*. Each chromosome has a short region appearing as a constriction, known as the *centromere*.

Metaphase:

The membrane around the cell nucleus disappears, and the pairs of chromatids come to lie on a plane through the center of the cell called the *equatorial plane*. A structure known as the *spindle* is formed, which appears as fibers running from the centromeres of each chromatid to one of two points at the poles of the cell known as *asters*. The two chromatids of each chromosome are attached to asters at opposite poles of the cell.

It is at this stage that the chromosomes are most distinct and can easily be counted.

Anaphase:

During anaphase the chromatids separate, at the centromeres first, and then move to the respective poles of the spindle. Each chromatid can now be considered to be a separate chromosome. It will replicate during interphase to form a second chromatid so that the mitotic cycle can be repeated.

Telophase:

The chromosomes have now reached the poles, and a nuclear membrane forms around each daughter nucleus. In the final stage of telophase the cell protoplasm divides (cytokinesis), and a wall forms around each of the two daughter cells.

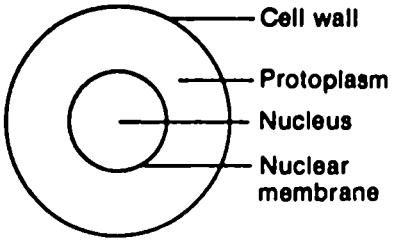
The prophase and telophase stages of mitosis are relatively long processes, whereas metaphase and anaphase are commonly very short. The whole process of mitosis may take only a few hours or up to 2 or 3 days, depending on the organism and on environmental conditions.

Meiosis

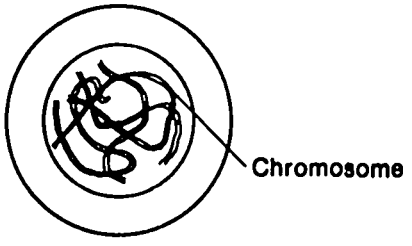
Each of the parent cells has the diploid number of chromosomes (2n). During the formation of the pollen grains and ovules a form of division known as reduction division, or *meiosis*, occurs, producing pollen and ovules with only half this number (n)—the haploid number. When fertilization takes place, the nucleus of a pollen grain combines with the nucleus of an ovule to form the zygote: the n chromosomes from the pollen combine with the n chromosomes from the ovule and the resulting zygote has the diploid number of chromosomes (2n), like the rest of the cells (Fig. 3.2).

The cells that have n chromosomes—the haploid number, which will combine on fertilization—are called *gametes*. In plants, the male gametes are the

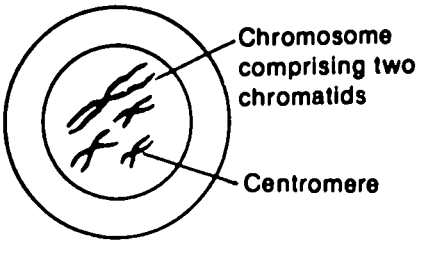
1. Interphase: The stage between mitotic divisions.



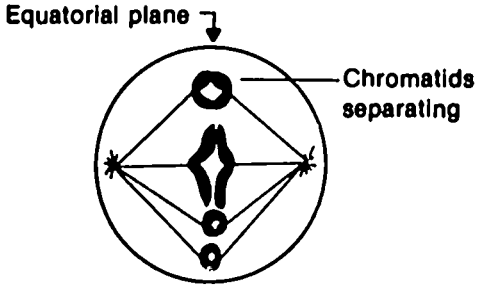
2. Early prophase: The chromosomes become visible as long threadlike structures.



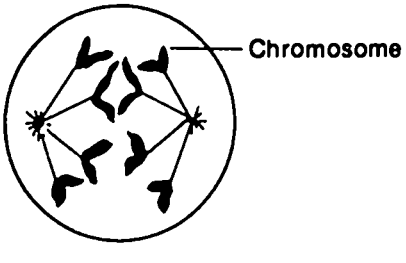
3. Late prophase: The chromosomes shorten and become more distinct. Each chromosome can be seen to consist of two chromatids.



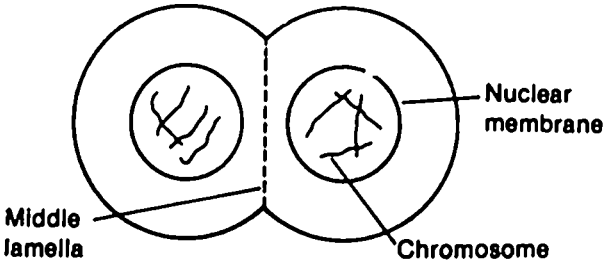
4. Metaphase: The nuclear membrane disappears and the spindle forms. The chromosomes become arranged on the equatorial plane and can be seen clearly.



5. Anaphase: The two sets of daughter chromosomes begin to elongate as they approach the opposite poles of the cell.



6. Telophase: The chromosomes have reached the poles, and a nuclear membrane forms around each nucleus. A cell wall (the middle lamella) forms between the two daughter cells.



7. Interphase: The two daughter cells are now fully formed. The chromosomes are no longer visible.

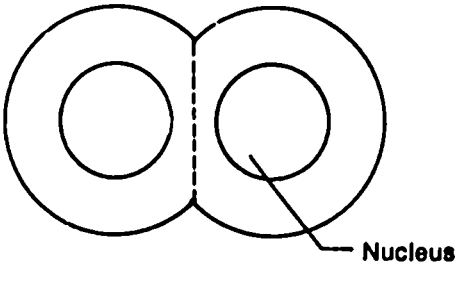


Figure 3.1: The stages of mitosis.

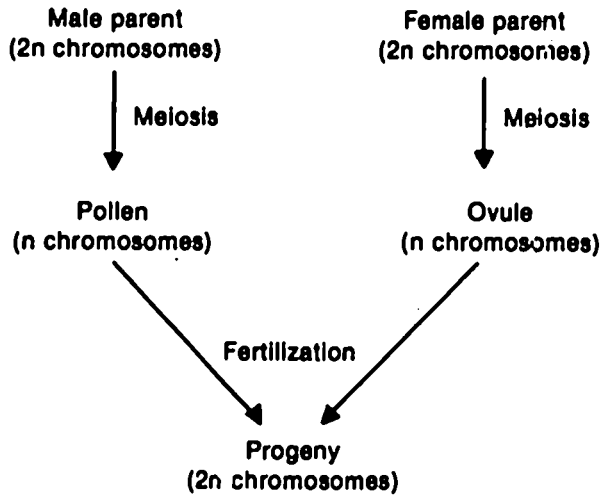


Figure 3.2: Meiosis.

pollen grains and the female gametes are the ovules (or, more correctly, the egg cell in the ovule).

Meiosis consists of two phases: meiosis 1, during which the parent cell divides to form two daughter cells, each having only half the number of chromosomes; and meiosis 2, which is very similar to mitosis except that the cells concerned have only the haploid number of chromosomes. These two divisions are shown in Figure 3.3.

In both meiosis 1 and 2, the prophase, metaphase, anaphase, and telophase stages can be recognized, as in mitosis. Figure 3.4 shows the stages of meiosis, which can be summarized as follows:

Process of Meiosis

Prophase 1:

This extended stage is often subdivided into several other stages. In the diploid cell, one set (n) of chromosomes has been derived from the male parent and one set (n) of chromosomes has been derived from the female parent. The two sets are exact duplicates; thus each chromosome in the diploid cell has a counterpart that is identical in structure, length, and position of the centromere, and each allele has a corresponding allele on the other chromosome. Such a pair of chromosomes is known as *homologous* chromosomes.

During prophase 1, the chromosomes become visible as threadlike structures and homologous chromosomes come to lie side by side, so that each segment of the chromosome pairs with the corresponding segment of its homologous partner. When they are paired in this way, the two chromosomes are known as a *bivalent*. Each chromosome divides lengthwise to form two *chromatids* that are joined at the *centromere*, and the pairing force between the chromosomes ceases, but they remain joined at one or two places along their length. The place where two chromosomes remain joined is called a *chiasma*.

Near the end of prophase 1, the chromosomes become very short and distinct.

Metaphase 1:

The nuclear membrane dissolves, the chromosomes come to lie on the equatorial plane, and the spindle is formed.

Anaphase 1:

One chromosome (still having two chromatids) of each homologous pair moves to one pole and the other chromosome moves to the other pole, along the spindle fibers.

Telophase 1:

When the chromosomes have reached the poles, nuclear membranes form around them and *cyto-*

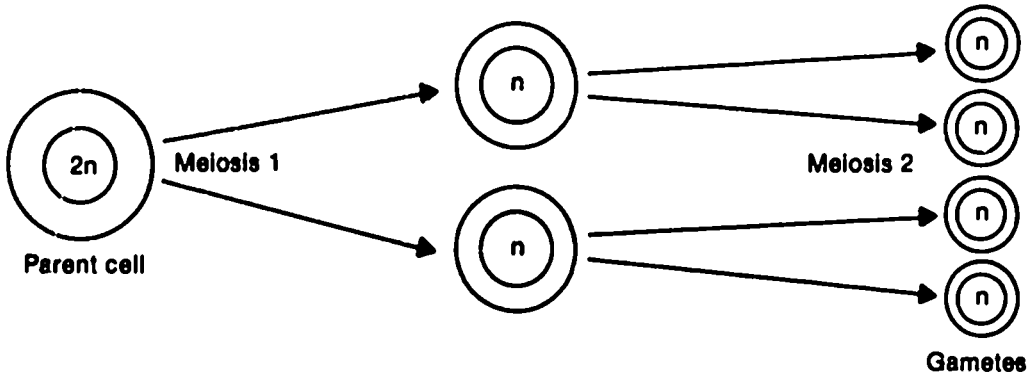
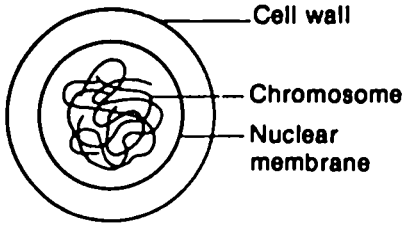
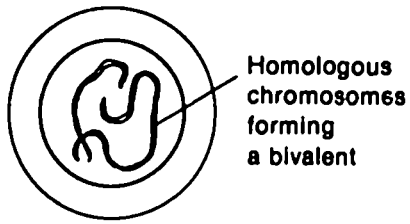


Figure 3.3: The two phases of meiosis.

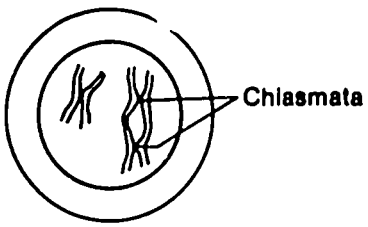
1. Very early prophase 1: The chromosomes become visible.



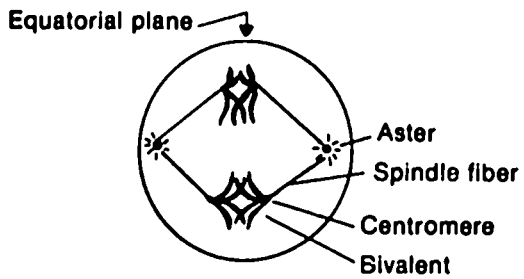
2. Early prophase 1: Homologous chromosomes pair to form bivalents



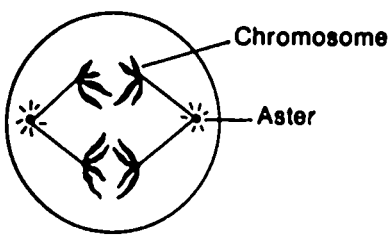
3. Late prophase 1: The homologous chromosomes in each bivalent separate, being held together only at chiasmata.



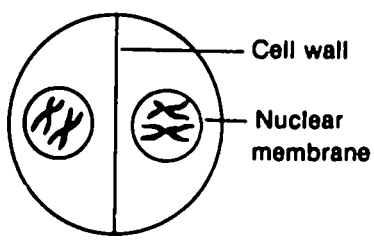
4. Metaphase 1: The chromosomes come to lie on the equatorial plane and are attached to the spindle. The nuclear membrane disappears.



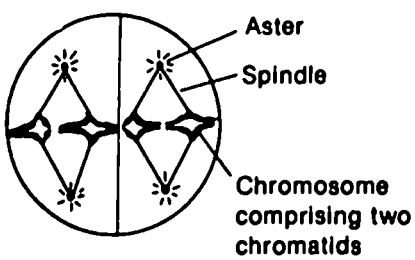
5. Anaphase 1: The chromosomes, each comprising two chromatids, move to opposite poles, the centromeres leading.



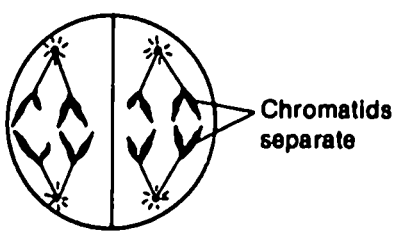
6. Telophase 1: A nuclear membrane forms around each set of chromosomes. Cytokinesis takes place.



7. Metaphase 2: The nuclear membrane disappears again and the chromosomes in each cell come to lie on the equatorial plane and are attached to the spindle.



8. Anaphase 2: The chromatids separate and move to opposite poles, as in mitosis.



9. Telophase 2: Nuclear membranes form around each of the nuclei, and cytokinesis takes place to form four daughter cells.

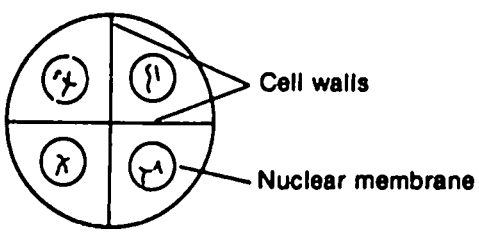


Figure 3.4: The stages of meiosis.

kinesis (the division of the cell) generally takes place.

Interphase:

There may be a short interphase, but generally the second division of meiosis follows almost immediately, simultaneously in both cells.

Prophase 2:

This is a short stage, and the chromosomes, already visible, soon pass into metaphase 2.

Metaphase 2:

The nuclear membrane disappears and the chromosomes line up on the equatorial plane.

Anaphase 2:

The chromatids separate and move to opposite poles.

Telophase 2:

Having reached the poles, each of the four groups of chromosomes becomes enclosed in a nuclear membrane. A second cytokinesis takes place and four daughter cells are formed, each with n chromosomes.

Gametogenesis and Fertilization

The formation of the gametes (the pollen and egg) is known as *gametogenesis*.

Formation of the Male Gametes: In the young anthers, there are a number of diploid cells known as *pollen mother cell* that divide by meiosis to form the haploid pollen grains. Each pollen mother cell forms four pollen grains. The haploid nucleus in each pollen grain then undergoes a further division by mitosis, resulting in each pollen grain having two nuclei: the *generative nucleus* and the *tube nucleus*. In sorghum the pollen is in this binucleate stage (binucleate = having two nuclei) when the anthers *dehisce* (shed their pollen).

Formation of the Female Gametes: The ovule consists of a number of cells, only one of which (the egg) is correctly the female gamete. In each ovule, a diploid cell known as the *embryo-sac mother cell* divides by meiosis to form four haploid cells called the *embryo-sac initials*. Three of these cells die, and the nucleus in the remaining haploid cell divides three times by mitosis to form a cell called the *embryo-sac*, which has eight haploid nuclei. Of these eight, one becomes the egg, the true female gamete; two of the nuclei unite to form a diploid nucleus (which later produces the *endosperm nucleus*), and the five remaining nuclei have other functions. The development of the pollen and egg is shown in Figure 3.5.

Fertilization

After pollination, when the pollen grain is on the surface of the stigma, the generative nucleus divides again, by mitosis. At this stage, the pollen grain contains three haploid nuclei: the *tube nucleus* and the two *generative nuclei*. The pollen grain then germinates and produces a tube (the *pollen tube*), which grows down the style and enters the embryo-sac through a small hole called the *micropyle*.

Two separate fertilizations then take place: One of the generative nuclei unites with the egg to produce the diploid zygote; the other generative nucleus unites with the diploid endosperm nucleus to form a triploid (3n) nucleus.

After fertilization, the zygote grows by a series of mitotic divisions to form the embryo in the seed (the *cotyledons*, *radicle*, and *plumule*), and the triploid endosperm nucleus divides by mitosis to produce the endosperm tissue. In monocotyledons, the endosperm often forms the main bulk of the seed.

This process of *double fertilization* introduces genetic material from the pollen parent into both the embryo and the endosperm. The influence of the genes from the pollen parent on the endosperm is called *xenia* and may affect such characters as endosperm color (for example, yellow seeds on a white-seeded ear of corn).

In addition to the embryo (2n) and endosperm (3n) tissue in the seed, unfertilized diploid cells from the ovule also divide by mitosis to form part of the seed (the *testa*), and such tissue is unaffected by genes from the pollen parent.

Single-Factor Inheritance

Basic Laws

The basic laws of genetics were first discovered by Gregor Mendel, who published his findings in 1865. His work received no recognition at the time, however, and it was not until 1900 that Mendel's laws were rediscovered, independently, by de Vries in Holland, Correns in Germany, and Tschermark in Austria.

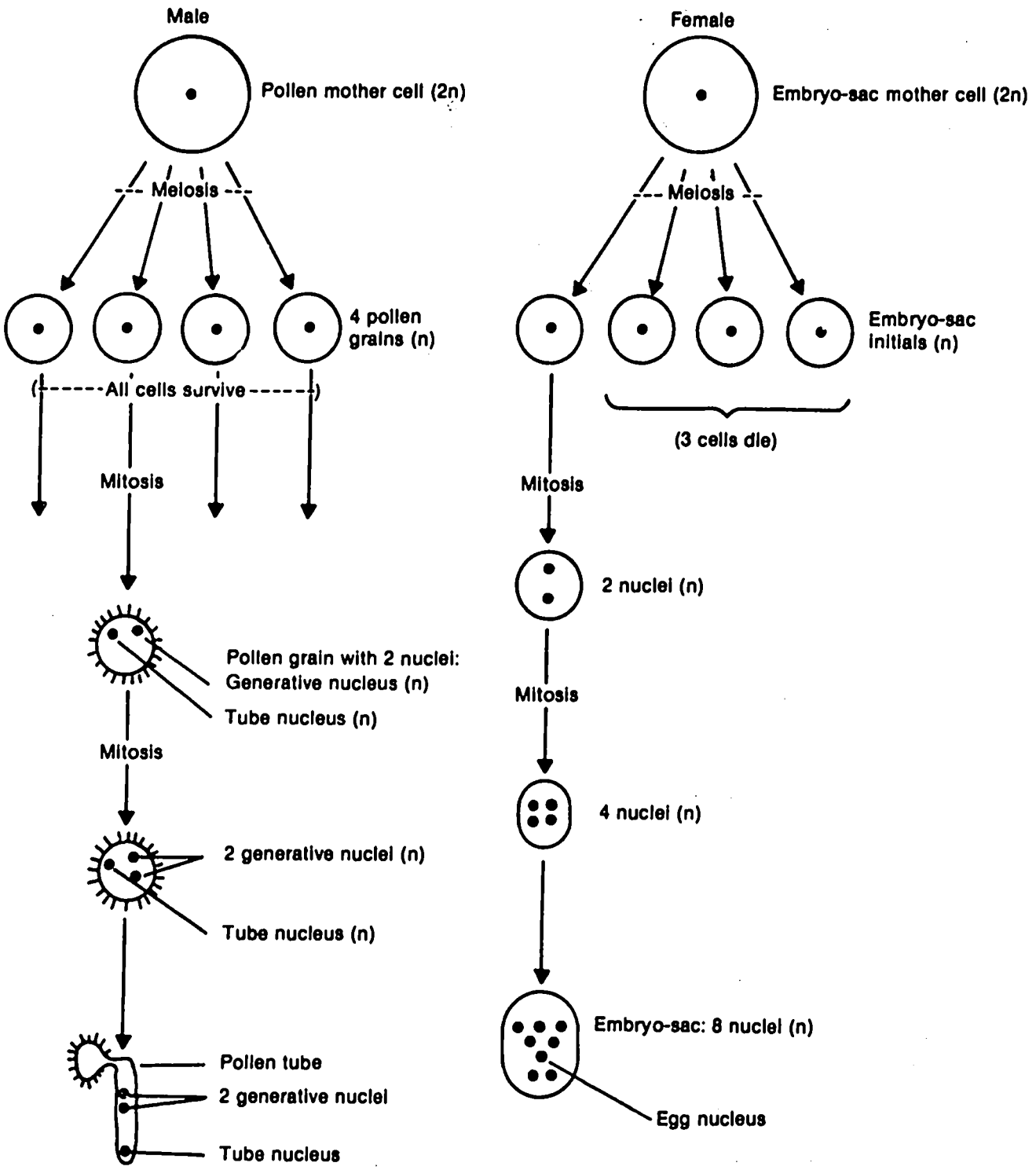


Figure 3.5: Gametogenesis in plants.

Mendel's success was due largely to the fact that he systematically studied the inheritance of single characters, one at a time, in his crosses, and that he started with lines that bred true (what were subsequently called homozygous lines). For example, he studied seven pairs of contrasting characters in garden peas and found the inheritance of each pair to be similar. These characters were:

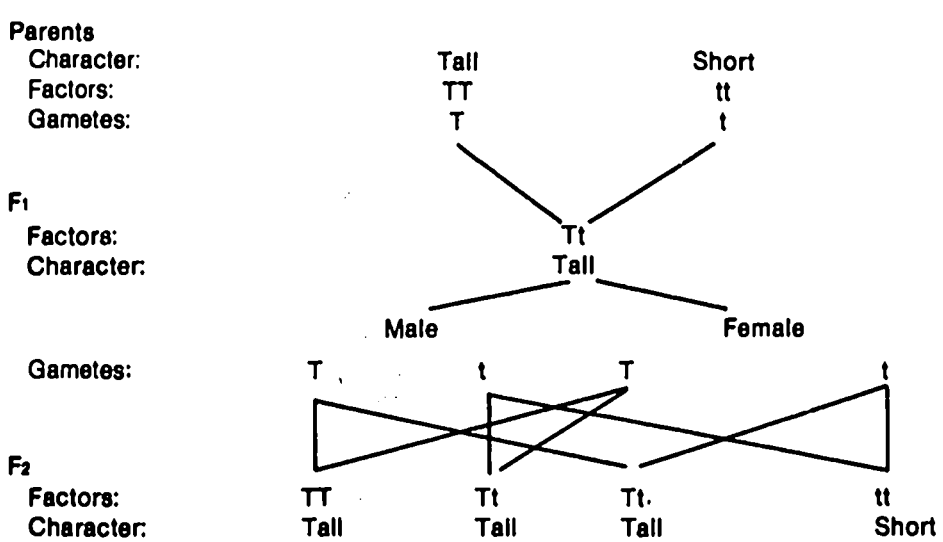
Tall and short growth habits
Green and yellow pods
Constricted and inflated pods
Indeterminate and determinate growth habits
Yellow and green cotyledons
Smooth and wrinkled seed coats
White and grey seed coats

Mendel crossed a tall plant with a short plant and found that the offspring were all tall. The generation following a cross between two parents is called the *first filial generation*, or more simply, the F_1. In this generation, the character that expresses itself is called the *dominant* character, and the parental character that is not expressed in the F_1 is called the *recessive* character. Thus, in Mendel's cross the tall growth habit was found to be dominant; the short habit was recessive. Similarly, in other crosses, Mendel found that green pods were dominant and yellow pods recessive; indeterminate growth habit was dominant and determinate growth habit was recessive, etc.

The next generation, the F_2, was obtained by selfing the F_1 plants (garden peas are normally self-pollinated), and in this generation Mendel found both parental characters were represented. In the F_2 of the cross of tall plants with short, he found 787 tall plants and 277 short plants. Similar ratios of approximately 3:1 for the dominant:recessive character were found for all seven pairs of characters. The appearance of both types of plants in the F_2 is called *segregation*.

To explain these findings, Mendel considered each character to be controlled by units called *factors*; he found that an individual plant had two such factors for each character. When plants were crossed, one factor was contributed by each parent to the F_1 generation. If the parents had different characters, the two factors in the F_1 would be different and (generally) one of the factors would express itself and suppress the expression of the other factor (Fig. 3.6). The factor expressed in the F_1 is the dominant factor; the suppressed unit is the recessive factor. When F_1 plants reproduce, the contrasting factors separate, or *segregato*, during the formation of the gametes, and thus two kinds of gametes are produced. When fertilization takes place, gametes may combine either with a gamete of their own kind or with a gamete bearing a contrasting factor.

When gametes are formed by a heterozygous plant, half the gametes will contain one of the factors and the other half will contain the other factor. (Half the pollen grains will carry the factor for tallness and the other half will bear the factor for shortness.) When fertilization occurs, there is an equal chance for either factor in the pollen to combine with either factor in the egg. Thus, each of the four



The phenotypic ratio in this case is 3 tall:1 short.

Figure 3.6: The generations following a cross between a tall and a short plant based on a cross by Mendel.

F_2 combinations has an equal chance of occurring (Fig. 3.6). If a large number of F_2 plants is studied, the ratio of the tall plants to the short plants will be very close to 3:1. If only a few plants are studied, however, the exact ratio may differ somewhat from this ratio. Figure 3.6 shows that in the F_2 population, three tall plants are produced for each short plant. Only a third of the tall plants, however, have the pair of factors TT, and the other two-thirds have contrasting factors Tt; but the plants are still tall because the factor for tall growth habit (T) is dominant to the recessive factor (t) for shortness.

Symbols

It is a convention in genetics that the symbol used for a dominant factor is written with a capital letter, while the recessive factor takes the same letter but is small (lower case). Thus Ms_3 is dominant for male-sterility; ms_3 is recessive for male-sterility. Likewise Dw_1 is a dominant factor for plant height and dw_1 is recessive. (The genes are numbered sequentially when more than one gene controls the same trait in a plant type.)

If an individual plant has the same two factors for a character (e.g., Ms_3 Ms_3, ms_3 ms_3, Dw_1 Dw_1, or dw_1 dw_1), it is called *homozygous* for that character, but if the factors are different (Ms_3 ms_3, Dw_1 dw_1, etc.) it is called *heterozygous* (Fig. 3.7.)

Alleles

In genetics, the factors as described by Mendel are now called alleles, and it has been shown that (for most practical purposes) alleles usually behave in a manner similar to Mendelian factors. A pair of alleles controlling a character is located on a homologous pair of chromosomes, with one allele located on each. At meiosis 1, when the chromosomes separate, one allele is carried on each chromosome

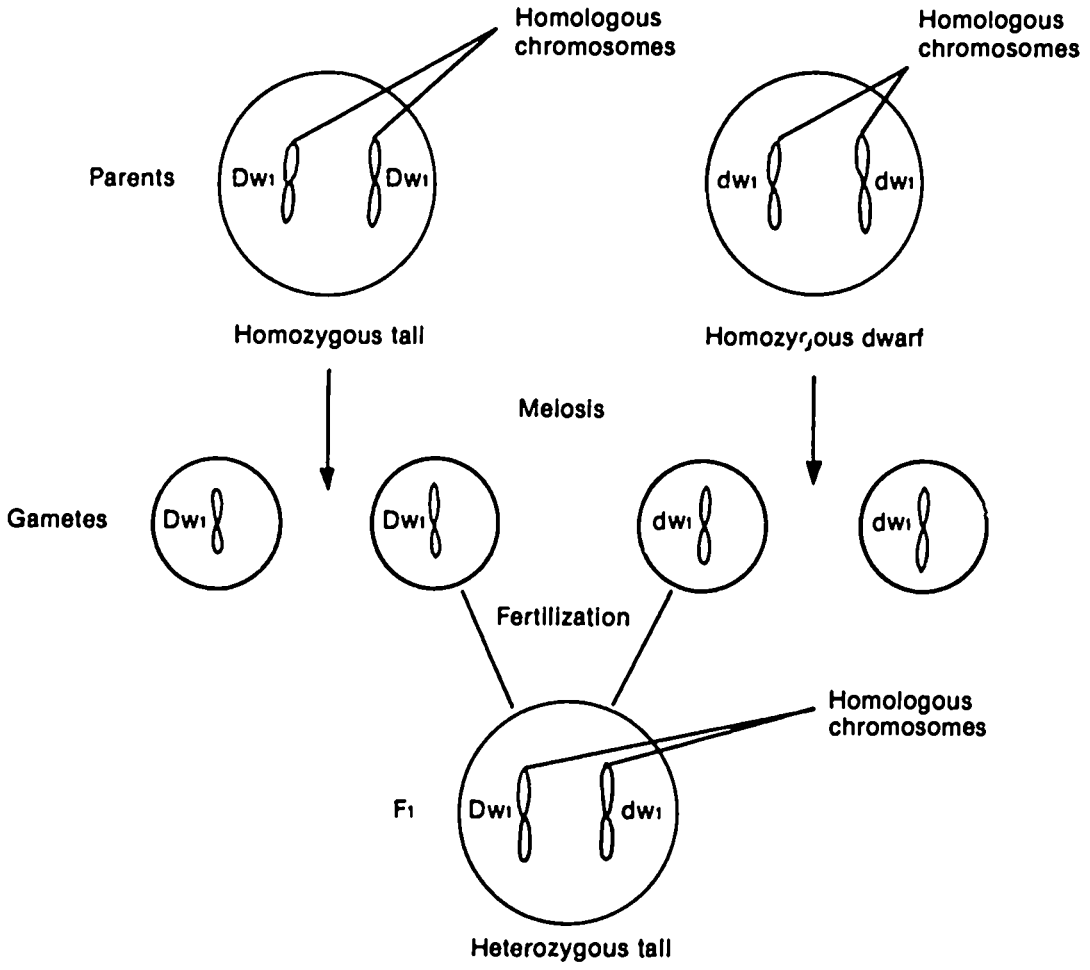


Figure 3.7: The separation and combination of a pair of factors during the formation of gametes and fertilization.

into the haploid cell. Thus the gametes have only one allele of the pair.

The genetic constitution of the plant is called the *genotype*. In the cross discussed, three different genotypes were shown: TT, Tt, and tt. The *phenotype* of the plant is the observed character of the plant, and in this example there were only two phenotypes: tall and short.

In the F_2 generation (Fig. 3.6) there is a 3:1 ratio in the phenotype (three tall:one short), with the dominant character (tall) being the main class. This ratio is referred to as the *phenotypic ratio*. The three possible genotypes, however, are in the ratio 1TT:2Tt:1tt; this is called the *genotypic ratio*. Plants having different genotypes may have the same phenotype, as both TT and Tt result in tall plants.

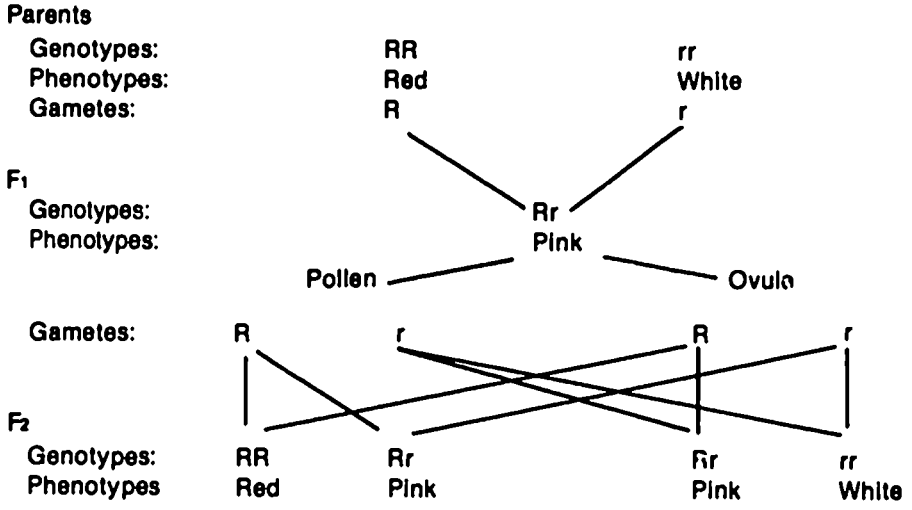
3.8. The phenotypic ratio in this case is one red:two pink:one white. The genotypic ratio is 1RR:2Rr:1rr.

Segregation

If a plant is homozygous for a particular character, all the gametes bear the same allele, and self-fertilization in this case results in the progeny being the same as the parent.

If a plant is heterozygous for a particular character, it will not breed true on selfing, because two types of gametes are produced: the dominant and the recessive (Fig. 3.9).

This process through which a heterozygous plant produces several different genotypes is called *segregation*.



The phenotypic ratio in this case is 1 red:2 pink:1 white, and the genotypic ratio is 1 RR:2 Rr:1 rr

Figure 3.8: Cross involving a single pair of alleles where the heterozygous plant has an intermediate phenotype.

A 3:1 phenotypic ratio and 1:2:1 genotypic ratio are typical of the inheritance of characters controlled by a single gene with one allele dominant to the other.

Intermediate Phenotypes

In some cases, one allele is not dominant to the other, and the heterozygous plant may have a phenotype that differs from both of the homozygous parents. In some species, a cross between a homozygous red flower (RR) and a homozygous white flower (rr) will result in a heterozygous F_1 (Rr) that may be pink. This situation is illustrated in Figure

Testcross

A plant that has the recessive phenotype (e.g., dwarf) must have the homozygous recessive genotype (dw_1dw_1). A plant having the dominant phenotype (tall) may be either homozygous dominant (Dw_1Dw_1) or heterozygous (Dw_1dw_1). To test whether a plant is homozygous tall (dominant) or heterozygous, a *testcross* can be made that involves crossing the plant with the homozygous recessive (Fig. 3.10).

If the plant were homozygous, all the F_1 plants would be tall, but if the plant were heterozygous, half the plants would be tall and half would be dwarf.

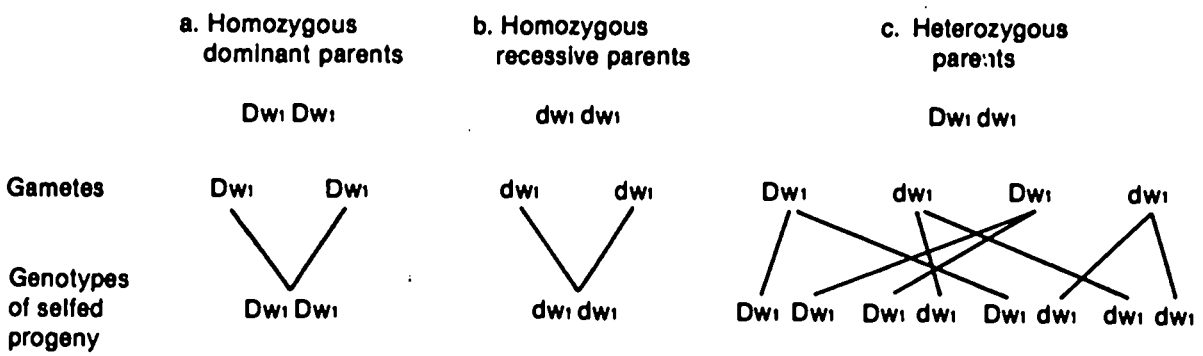


Figure 3.9: Selfing in homozygous and heterozygous plants.

Reduction of Heterozygosity by Selfing

If two parents, one homozygous for the dominant and one homozygous for the recessive traits, are crossed, all the F_1 plants will be heterozygous. If the F_1 generation is selfed, half the plants in the F_2 are homozygous Dw_1Dw_1 and dw_1dw_1 and half are heterozygous Dw_1dw_1. In the F_3 generation produced by selfing the F_2, the homozygous plants continue to breed true and the heterozygous plants produce one-half homozygous and one-half heterozygous progeny. Thus, in the F_3 generation, only one-quarter of the plants are heterozygous and three-quarters are homozygous (Fig. 3.11).

In each successive generation of selfing, the proportion of heterozygous plants is reduced by 50%. In plant breeding, the production of pure-line varieties (homozygous varieties that breed true) is achieved by selfing plants for a number of generations (usually five to eight) until heterozygosity is reduced to a very low level.

In an F_8 population, the proportion of heterozygous plants will be only 0.78%.

Backcrossing

Backcrossing is essentially a process of gene transfer from one line to another. With each generation of backcrossing, the genetic composition of the donor (*nonrecurrent* parent) is reduced by a factor $(½)^n$, where "n" is the number of generations of backcrossing. For example, after the second generation of backcrossing, the genetic contribution of the nonrecurrent parent to the progeny has been reduced to one-fourth; $(½)^2 = ¼$. After the third generation the contribution has been reduced to ⅛, etc. During the backcrossing program, selection is for the character desired from the nonrecurrent parent. After five to seven generations of backcrossing, the original line (*recurrent* parent) has been recovered, with the addition of the character from the nonrecurrent parent.

Suppose that a single dominant gene "AA" from a source line (nonrecurrent parent) is to be transferred into an elite agronomic line (recurrent parent) with the recessive gene "aa." The first cross, AA x aa, results in the F_1 Aa. The F_1 is then crossed with

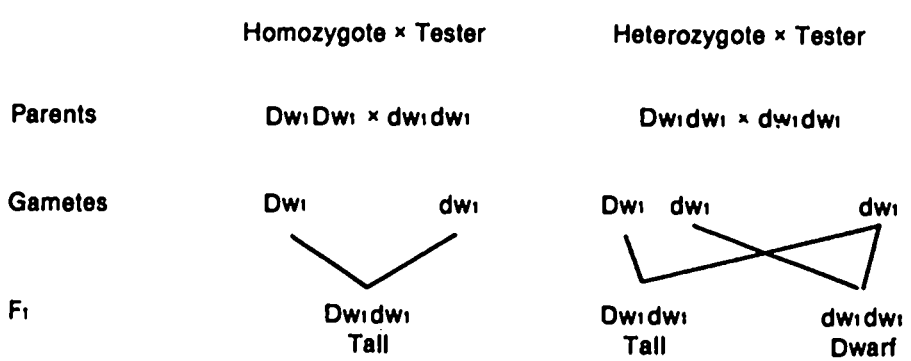


Figure 3.10: Testcross.

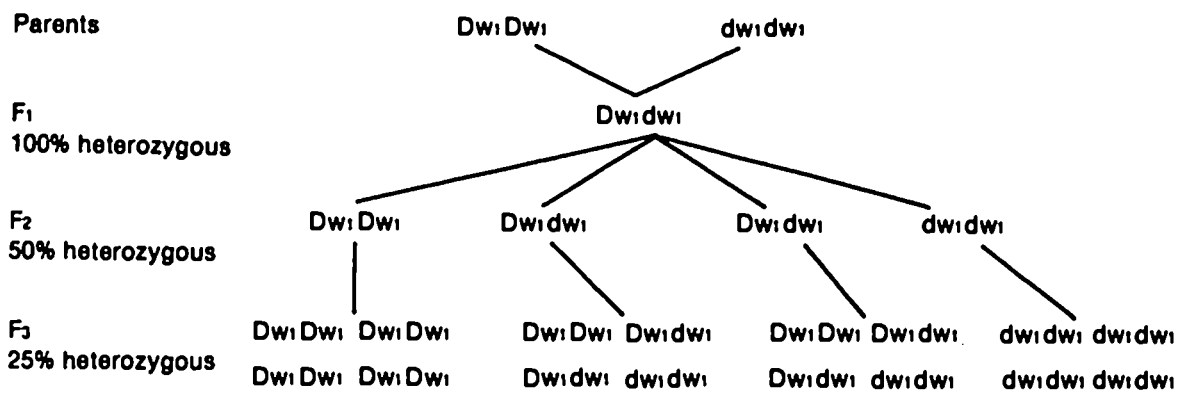


Figure 3.11: Reduction in heterozygosity by selfing.

the recurrent parent aa; i.e., F_1 x aa produces the BC_1. The progeny of the BC_1 are one-half Aa and one-half aa:

		Gametes from recurrent parent	
		a	a
Gametes from F_1	A	Aa	Aa
	a	aa	aa

The second backcross would be made only to the Aa plants; i.e., Aa segregates from the BC_1 generation are crossed with recurrent parent aa. It is apparent that the progeny from this cross (BC_2) will also be one-half Aa and one-half aa. The process of backcrossing each generation to the Aa parent is continued until the recurrent parent is recovered with the trait A in its genotype.

The problem is slightly more complicated when the trait to be transferred is recessive rather than dominant. The trait (A), when dominant, is expressed phenotypically in the heterozygote Aa; but when the trait is recessive (a) it is not expressed in the heterozygote Aa. If backcrossing is continuous, only a few progeny will be aa after several generations—it is necessary to self-pollinate after every one or two generations of backcrossing to identify the recessive segregate in the F_2. Backcrossing then continues only on the plants showing the recessive trait. Assume that a recessive trait "a" is to be transferred into an agronomically elite line.

The F_1 is made by crossing parent 1 (AA) with parent 2 (aa):

AA x aa forms the F_1 Aa, or $P_1 \times P_2 \longrightarrow F_1$

The first backcross is made by crossing the F_1 with P_1:

		Gametes from P_1	
		A	A
Gametes from F_1	A	AA	AA
	a	Aa	Aa

The progeny in the first backcross (BC_1) are 2AA:2Aa, or in the ratio 50% AA to 50% Aa, and all progeny show the dominant trait. The progeny from the BC_1 should then be selfed. From the AA parents will come four AA progeny; from the Aa parents will come 1AA:2Aa:1aa.

	BC_1 homozygous	
	A	A
A	AA	AA
A	AA	AA

	BC_1 heterozygous	
	A	a
A	AA	Aa
a	Aa	aa

The total progeny are five + AA + one aa + two Aa, or seven progeny showing the dominant trait A to one showing the recessive trait a.

The second backcross is made by crossing P_1 (AA) to the recessive (aa) segregate from the BC_1 F_2 (or aa x AA), to produce the BC_2 (Aa). The process is repeated until the original phenotype is recovered with the aa trait.

If the character to be transferred is controlled by many genes (polygenic, or quantitative inheritance), it is probably not possible to backcross for more than one or two generations before a new line must be selected by a pedigree-breeding method. This is because there are so many genes segregating that it is not possible to recover individuals among the backcross or F_2 segregates that have all the genes contributed by the source, or nonrecurrent parent. As some of the genes from the quantitative trait are lost, the expression of the trait becomes less, and continuous backcrossing is not possible.

Backcrossing is useful for several breeding objectives. Examples include insect, disease, or drought resistance, and high lysine or protein content. As a first step, appropriate sources must be found. Usually, these should be sought first from large collections of diverse material, rather than by conducting tests on only a few highly selected agronomic lines. After sources are found, determination should be made of the mode of inheritance and/or whether dominance is involved, especially if the character is controlled by only a few genes. This information should be useful for determining the breeding procedures (especially the number of backcrosses that can be made) and should be valuable for selecting nonrecurrent parents in a backcrossing program.

As a breeding procedure, backcrossing is used to transfer a desirable character or characters to another (usually agronomically superior) line. Whether or not the desired line can be recovered with only the change(s) desired depends on the number of genes controlling the character(s) to be transferred and their relationship to other genes (see Linkage, p.42). The fewer the number of genes and the better the character is expressed, the greater is the chance of recovering the original type with the added character(s).

Any given character need not necessarily have the same mode of inheritance—there may be differences between varieties. It would generally be expected that the variety with the lowest gene number or the greatest dominance effect would be easiest to use in a backcrossing program. If 15 or 20 lines are found to be resistant to a certain disease, it might be worth investigating the inheritance of the resistance in these lines—one or two of the varieties may be much better than others for use in a backcrossing program.

The relationship between the recurrent parent and nonrecurrent parent is an important consideration. For example, if a desired character is found in both a kafir and a durra type, and it is desired to transfer this character to a kafir, then it would be better to use the kafir rather than the durra source as the nonrecurrent parent. Use of the kafir in this case might make it possible to recover a line more nearly like the one desired (and more quickly). This is a worthwhile point to consider when choosing parents for a backcrossing program.

Independent Assortment

In addition to single-character studies, Mendel studied inheritance in crosses between parents that differ with respect to two characters. An F_1 resulting from crossing two parents that differ by a single character is called a *monohybrid*, and an F_1 produced by crossing parents that differ by two characters is called a *dihybrid*.

Dihybrid Segregation

In a cross between a plant with round and yellow seeds and a plant with green and wrinkled seeds, Mendel found that the F_1 generation had round and yellow seeds. The characters round and yellow are thus dominant, and green and wrinkled are recessive.

In the F_2 derived from selfing the F_1, four combinations of phenotypes appeared in the following numbers:

315 round yellow
108 round green
101 wrinkled yellow
32 wrinkled green

Taking the two pairs of characters separately, it can be seen that there were 423 round, 133 wrinkled, 416 yellow, and 140 green. Both these ratios are approximately 3:1, the usual ratio for a character controlled by a single gene.

The four phenotypic combinations are a result of two 3:1 ratios being superimposed and represent a 9:3:3:1 ratio. This can be demonstrated as follows:

		Round	wrinkled
		3	1
Yellow	3	9	3
Green	1	3	1

The largest class (round and yellow) contains both the dominants; the intermediate classes have

one dominant character (round + green or yellow + wrinkled), and the smallest class is homozygous recessive for both characters (wrinkled green).

Such results are obtained when the two pairs of characters behave independently; this is known as *independent assortment* and results in equal numbers of YR, Yr, yR, and yr gametes. Figure 3.12 shows how independent assortment occurs with respect to genes on chromosomes.

Figure 3.13 shows how the F_1 gametes can combine to produce the different F_2 classes. The four types of female gametes are written along the top of a table known as a *checkerboard*, and the four male gametes are written down the side. The body of the checkerboard shows the genotypes produced by the union of each of the male gametes with each of the female gametes. Since there is an equal chance of each gamete being produced, there is an equal chance for the genotype in each square to occur. Thus if a particular genotype is present in two separate squares (e.g., RRYy), this genotype is twice as likely to be produced in the F_2 population as a genotype that is to be found in only one square (e.g., RRyy).

Figure 3.13 shows that the 16 squares in the checkerboard give rise to nine different genotypes. These genotypes, together with the genotypic ratios, phenotypes, and phenotypic ratios, are as follows (Fig. 3.14).

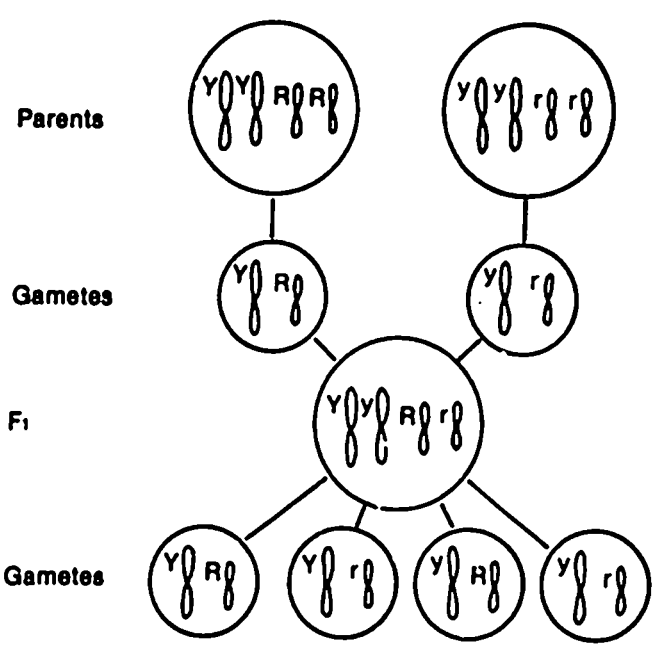


Figure 3.12: Independent assortment of genes.

		Female gametes			
		RY	Ry	rY	ry
Male gametes	RY	RRYY	RRYy	RrYY	RrYy
	Ry	RRYy	RRyy	RrYy	Rryy
	rY	RrYY	RrYy	rrYY	rrYy
	ry	RrYy	Rryy	rrYy	rryy

Figure 3.13: The F_2 generation of a selfed dihybrid F_1 (genotype RrYy).

Genotype	Genotypic ratio	Phenotype	Phenotypic ratio
RRYY	1	Round yellow	9
RRYy	2		
RrYY	2		
RrYy	4		
RRyy	1	Round green	3
Rryy	2		
rrYY	1	Wrinkled yellow	3
rrYy	2		
rryy	1	Wrinkled green	1

Figure 3.14: Genotypes and phenotypes of F_2 plants from a dihybrid F_1.

Dihybrid Testcross

Earlier it was shown that the genotype of a plant can be determined by making a testcross—a cross with a homozygous recessive plant. The same procedure can be used to determine the genotype of a plant with respect to two characters. The tester plant must, of course, be homozygous recessive for both characters (rryy).

If, for example, there is a need to know the genotype of a round and yellow-seeded plant, there are four possible genotypes:

RRYY, RrYY, RRYy, and RrYy.

The four testcrosses are outlined below:

- Parent RRYY: There is only one kind of gamete, RY:

Test plant gametes:		RY
	ry	RrYy

i.e., all the progeny are round and yellow.

- Parent Rr YY: There are two kinds of gametes, RY and rY:

Test plant gametes:		RY	rY
	ry	RrYy	rrYy

i.e., one-half the progeny are round and yellow, and one-half are wrinkled and yellow.

- Parent RRYy: There are two kinds of gametes, RY and Ry:

Test plant gametes:		RY	Ry
	ry	RrYy	Rryy

i.e., one-half of the progeny are round and yellow and one-half are round and green.

- Parent RrYy: There are four kinds of gametes, RY, Ry, rY, and ry:

Test plant gametes:		RY	Ry	rY	ry
	ry	RrYy	Rryy	rrYy	rryy

i.e., one-fourth of the progeny are round and yellow;
one-fourth are round and green;
one-fourth are wrinkled and yellow; and
one-fourth are wrinkled and green.

Thus by observing the phenotypes of the progeny of a testcross, the genotype of the parent can be determined.

Linkage

Linked Genes

Independent assortment does not always occur, and the ratios discussed above may not hold true.

Genes on the same chromosome can assort independently, like genes on separate chromosomes. Those on the same chromosome that do not act independently are said to be *linked*. Figure 3.15 shows what happens in the parent, F_1, and F_2 generations when two pairs of genes are completely linked and so do not assort independently, but behave as a single gene. In this case, only three (instead of nine) different genotypes are produced in the F_2 generation: AABB, AaBb, aabb, and these are in a 1:2:1 ratio.

When genes are not completely linked, however, the frequency of genotypes in the F_2 cited above is not found; this situation is due to a phenomenon called *crossing over*.

As an example, consider the cross between a dihybrid parent (AaBb) and a homozygous recessive parent (aabb). If the genes are not linked, then a 1:1:1:1 genotypic ratio is expected for the four genotypes AaBb, Aabb, aaBb, and aabb. If the genes are linked, however, one might find 180 AaBb, 27 Aabb, 23 aaBb, and 170 aabb. The most frequent genotypes (AaBb and aabb) are the result of normal gamete formation (Fig. 3.16), but the gametes that gave rise to the offspring with the genotypes Aabb and aaBb (known as *recombinant* genotypes, because the genes have recombined) are produced by crossing over. Linked genes can recombine both in a *coupling* situation, where the arrangement of alleles is both dominants in one chromosome and both recessives in the other (AB/ab), and a *repulsion* situation, where the arrangement is a dominant and a recessive in each homologue (Ab/aB).

Crossing Over

During late prophase, when each chromosome is seen to consist of two chromatids, a chromatid of one chromosome may be seen to be joined with the chromatid of the homologous chromosome. This is where crossing over has occurred, and the point of exchange is a *chiasma*. Figure 3.17 outlines crossing over in a coupling situation.

In some cases, several chiasmata may be formed and more than one segment of the chromatids may be interchanged.

Chromosome Mapping

The percentage of crossing over (called *cross-over* units or *map units*) serves as a measure of the relative distance between genes on a chromosome; it is measured as the percentage of recombinant genotypes in the progeny of a testcross.

In Figure 3.16 there are 50 recombinant genotypes (27 Aabb + 23 aaBb) in a total of 400 plants (50 + 180 AaBb + 170 aabb). Thus the percentage of crossing over is:

$$50/400 \times 100 = 12.5\%$$

If another gene, C, is found to be linked to genes A and B, the order of genes on the chromosome can be worked out. If, for example, the crossing-over percentage between A and C is 6.5%, and between B

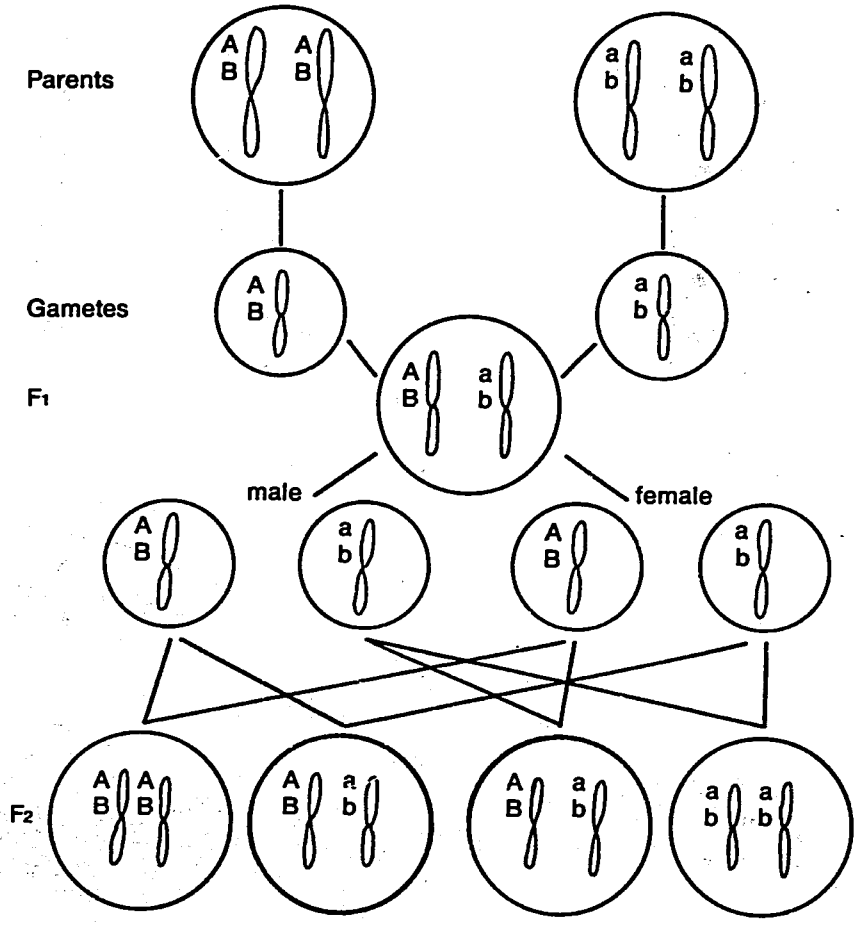


Figure 3.15: Linkage.

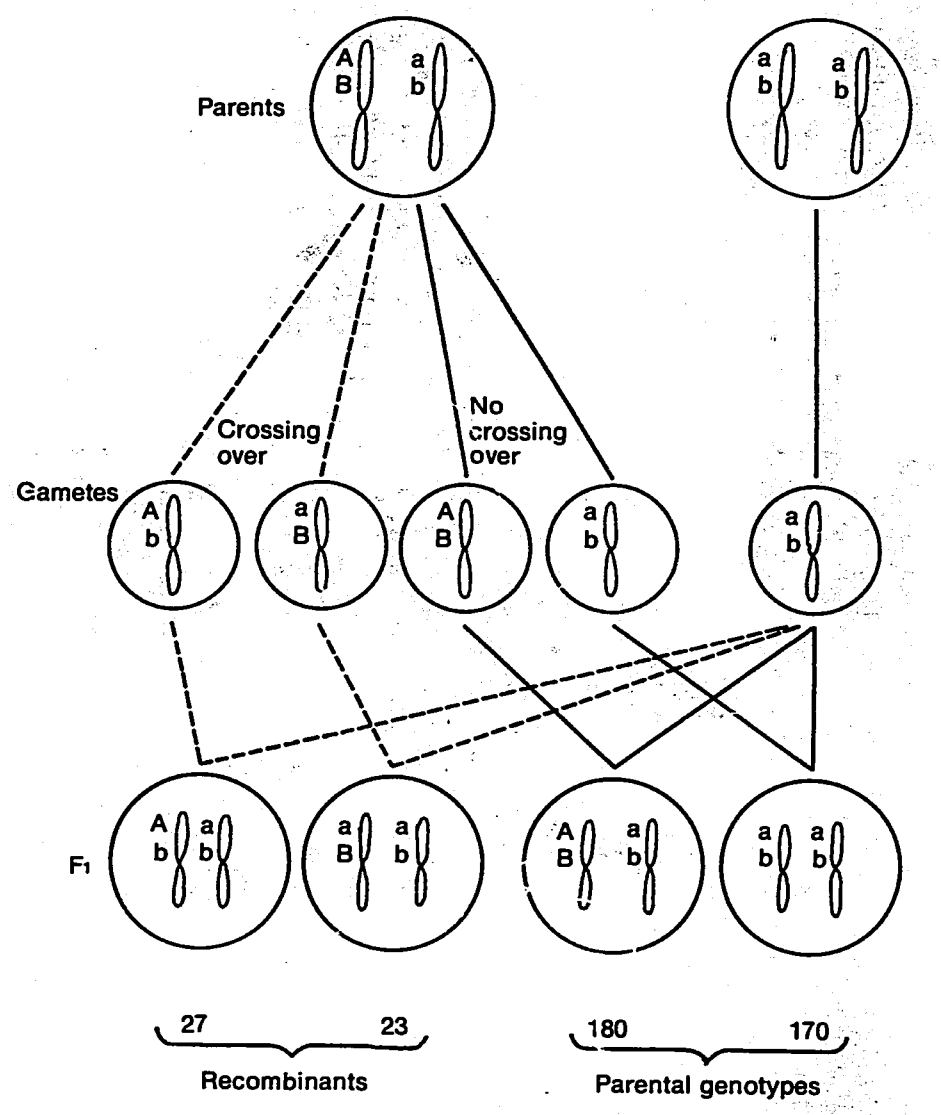
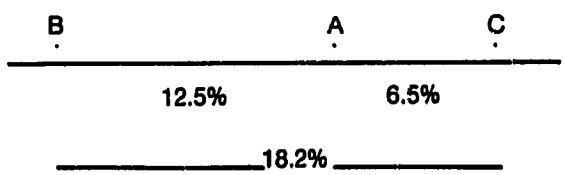


Figure 3.16: Dihybrid testcross with linked genes.

and C is 19%, then the order is BAC. Between B and C a low frequency of double cross-overs will give the parental genotype, so the number of cross-over units between them will be less than the sum of those between B and A and A and C. Note that two genes situated 50 or more cross-over units apart behave the same as nonlinked genes; i.e., the frequency distribution in the progeny would be AB, Ab, aB, and ab in equal frequency without linkage and with linkage of 50 cross-over units or more between A and B.



By studying linkage and the percentage of crossing over that occurs between linked genes, it is possible to assign the genes to groups, as well as to map the order of genes within groups. It may then be possible to locate groups of genes on specific chromosomes.

Pleiotropic Genes

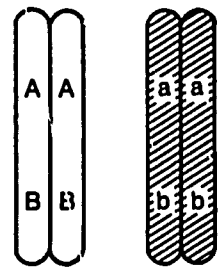
Some genes may influence the expression of more than one character; e.g., in sorghum, gene hl causes both an increase in the lysine content of storage proteins in the seed and a shrunken endosperm. Such genes are called *pleiotropic genes.*

It is often difficult to tell whether genes are truly pleiotropic or whether they are very closely linked. If genes are situated very close together on the chromosome, a large number of crosses may have to be made before a recombinant genotype is found. The presence of a single recombinant genotype, however, is sufficient to establish that two closely linked genes are involved and not a single pleiotropic gene.

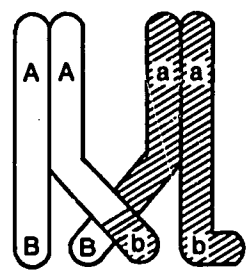
Two-Factor Inheritance

The basic model for the inheritance of a character controlled by two independent genes is the same as that given in Figures 3.12, 3.13, and 3.14 in the previous discussion. Consider the case in which flower color is controlled by genes at two loci, A and B. The homozygous recessive (aabb) produces white flowers, aaBB or aaBb produces red flowers, but the expression of dominant A depends on the genotype at locus B, so that with dominant B it produces

1. Homologous chromosomes, each composed of two chromatids lie side by side to form a bivalent:



2. As the chromosomes separate, points of contact can be seen, called chiasmata.(A single chiasma is shown here). Segments of the chromatids interchange at the chiasmata.



3. By the end of meiosis 2 the four chromatids are distributed, one in each of the haploid cells.

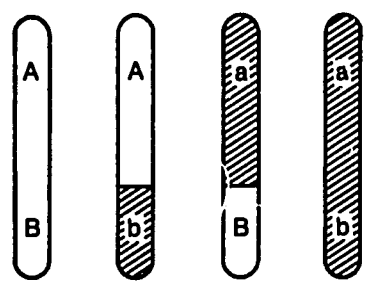


Figure 3.17: Crossing over.

purple flowers, but with recessive bb it produces pink flowers. This can be summarized as:

Genotype	Phenotype
aabb	White
A-bb	Pink
aaB-	Red
A-B-	Purple

The "-" in the genotype indicates that the allele can be either dominant or recessive, and it will have no effect on the phenotype; thus the genotype written A-B- can be AABB, AaBB, AABb, or AaBb, and in all cases the phenotype will be purple.

In a cross between two homozygous parents AABB (purple) x aabb (white), the F_1 generation will be heterozygous AaBb (purple).

The genotypes in the F_2 can be determined by the checkerboard method as follows:

		Female gametes			
		AB	Ab	aB	ab
Male gametes	AB	AABB	AABb	AaBB	AaBb
	Ab	AABb	AAbb	AaBb	Aabb
	aB	AaBB	AaBb	aaBB	aaBb
	ab	AaBb	Aabb	aaBb	aabb

Genotypes	Number	Phenotypes	Phenotypic ratio
AABB	1		
AABb	2	Purple	9
AaBB	2		
AaBb	4		
AAbb	1	Pink	3
Aabb	2		
aaBB	1	Red	3
aaBb	2		
aabb	1	White	1

Thus, the phenotypes in the F_2 are found in the ratio 9 purple : 3 pink : 3 red : 1 white. This ratio is typical of the inheritance of characters controlled by genes at two loci when there is no interaction between the genes concerned. Very often, however, the genes do interact and different ratios are produced. These ratios can be equated with the 9:3:3:1 ratio; for example an F_2 phenotypic ratio of 9:7 can be equated with a 9:(3+3+1) ratio. In this case, the genotypes with a dominant allele at both loci form one phenotypic class (9), and the genotypes with only one or no dominant allele all produce the same phenotype (7).

Genotypes	Number	Phenotypes	Phenotypic ratio
A-B-	9	Colored	9
A-bb	3		
aaB-	3	White	7
aabb	1		

Many types of gene interaction are possible, some of which are outlined below:

Complementary Genes: This type of interaction produces a 9:7 phenotypic ratio, as described above. The presence of two dominant alleles (A and B) is necessary for the expression of a character (e.g., red), and the absence of a dominant allele at either or both loci (A-bb, aaB- or aabb) results in the expression of an alternative character (white).

Modifying Genes: These genes alter the action of genes at another locus and have no action on their own. For example, if the genotype A- causes pink flowers and aa white flowers, the presence of dominant allele B at another locus may result in red flowers if A is also present, but will produce white flowers if A is absent. In this case, the genotype A-B- produces red flowers, A-bb produces pink flowers, and aaB- and aabb both produce white flowers. The phenotypic ratio here is 9 red : 3 pink : 4 white.

Inhibiting Genes: One gene may inhibit the expression of another gene, e.g., if A- produces a red flower color and aa white, the presence of a dominant allele B at another locus may suppress the action of A. Thus A-B-, aaB-, and aabb produce white flowers, and only A-bb produces red flowers. The phenotypic ratio in this situation is 13 white : 3 red.

Additive Genes: The presence of a dominant allele at either locus will give the same phenotype, and the effect is increased if there is a dominant allele at both loci. Thus, for example, if there are no dominant alleles (aabb) the plant is short, if there is a dominant allele at either locus (A-bb or aaB-) the plant will be intermediate in height, and if a dominant allele is present at both loci (A-B-) the plant will be tall. In this example the phenotypic ratio in the F_2 will be: 9 tall : 6 intermediate : 1 short.

Duplicate Genes: If a dominant allele is present at either locus or at both loci, the phenotype is the same. Thus A-B-, A-bb, and aaB- all result in the same phenotype, and only the homozygous recessive (aabb) is different. This type of gene action results in a 15:1 phenotypic ratio.

Masking Genes: The presence of a dominant allele at one locus may mask the effect of a dominant allele at the other locus. Suppose A- produces red flowers and aa white flowers, B- produces yellow flowers, and bb white flowers. When a dominant allele is found at both loci, the dominant allele A may

mask the effect of B. Thus, the genotypes A-B- and A-bb both produce red flowers, aaB- produces yellow flowers, and aabb produces white flowers. In this case the F_2 phenotypic ratio is 12 red : 3 yellow : 1 white.

The term *epistasis* originally was used to refer to gene interactions in which the genes at one locus (e.g., A) show dominance over genes at another locus (B). According to this definition, dominant modifying genes, inhibiting genes, and masking genes are all forms of epistasis.

More recently, the word has come to refer to all types of nonallelic gene interaction; i.e., all types of interactions that occur between genes at different loci.

Mutation

Mutations are sudden, heritable changes in the genetic material. They can be classified broadly into two main types, *chromosome mutations* and *gene mutations*.

Chromosome Mutations

Changes that occur in the structure of a chromosome are called chromosome mutations. In general, they have a harmful effect and often result in greatly reduced fertility or death of the plant. Many types of chromosome mutations may occur (Fig. 3.18).

- Duplication: When a small segment of a chromosome is added to the normal chromosome.
- Deficiency: When a segment of a chromosome is missing.
- Interchange: When a segment of one chromosome is interchanged with a segment of a nonhomologous chromosome.
- Translocation: When a segment of one chromosome is moved to another chromosome.
- Inversion: When a segment of a chromosome becomes detached and attaches again, but in a reversed position.

Gene Mutations

Changes in individual genes, called gene mutations, may be classified as:

1. dominant or recessive mutation,
2. beneficial or harmful mutation,
3. mutation occurring in somatic cells (normal diploid plant cells); or mutation occurring during the production of gametes.

If mutation takes place in somatic tissue during mitosis, all the cells derived from the mutant cells will carry the mutation. The plant tissue thus will contain a mixture of mutated and nonmutated cells. Such tissue is called a *mosaic*. These mutations are not carried over into the progeny (unless floral development subsequently occurs from mutated somatic tissue), unlike mutations that take place during the formation of the gametes.

Mutations are rare in nature, but there is generally a constant rate at which particular genes mutate; i.e., in maize, R, a color factor, mutates at a rate of about 500 per million gametes; I, a color-inhibiting gene, has a mutation rate of 100 per million gametes; and Sh (for shrunken grain) mutates at a rate of only 1 per million gametes.

Mutations from the dominant to the recessive state are the most common, and it is comparatively

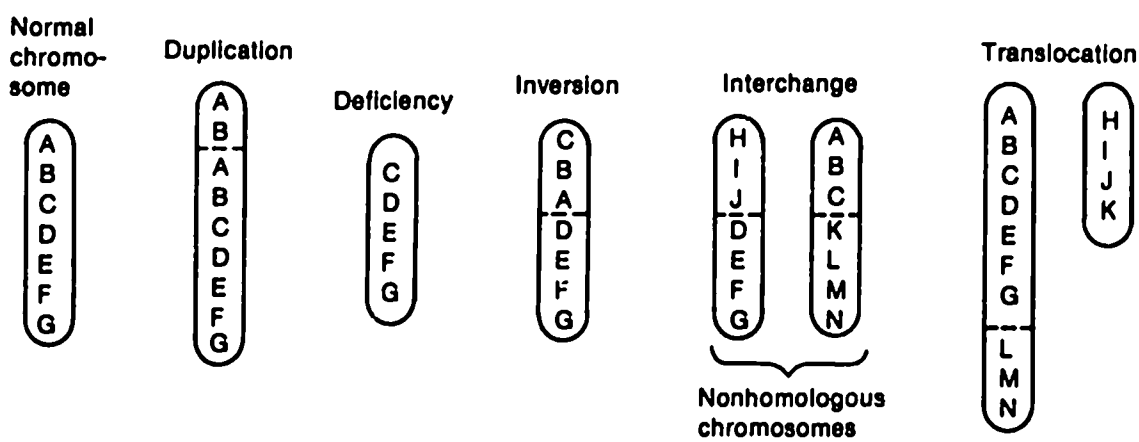


Figure 3.18: Chromosome mutations.

rare for a recessive allele to mutate to a dominant form. However, mutations are generally reversible, and if allele A mutates to a, then a can mutate back to A. But the mutation rate in the two directions may be different.

Because most mutations are recessive, they often do not show up in the first generation (called the M_1), but only if they are in the homozygous state in the M_2 or subsequent generation (Fig. 3.19).

Mutation is the main basis of evolution; it is the way in which new genes are formed. In general, most mutations are harmful and will not survive in a population. A few mutations are beneficial, however, and the mutant plant will then have a better chance of surviving under natural selection. Later, the mutant form of a gene may be found in many members of a species. When enough different mutations have built up in this way, a new species may be formed.

Mutation can be useful to the plant breeder as a source of new genes. Although the majority of gene mutations are harmful, the few beneficial mutations that occur can be used in the development of new improved genotypes. Chromosome mutations are rarely useful, however, and are almost always harmful.

Induced Mutation

Plant breeders may use several methods to increase the mutation rate. Both X-rays and gamma rays increase the mutation rate, but tend to cause a high percentage of harmful chromosome mutations. Low doses may cause a sufficient number of gene mutations to make this method of some value. Ultraviolet light is sometimes used and causes fewer chromosome mutations. Certain chemicals are known to increase the mutation rate, for example, ethyl methyl sulphonate (EMS). These chemicals produce a high gene mutation rate with relatively few chromosome mutations. (All mutagens are health hazards and should be treated accordingly.)

Ploidy

In sorghum, plants can have fewer or more than the diploid (2n) number of chromosomes. Those with half the diploid chromosome number are called *monoploids*. Those with more than the diploid number are called *polyploids*. In some cases, one or more chromosomes may be absent, or three or more of a particular chromosome may be found; such plants are called *aneuploids*. Some species have multiples of the *genome* (haploid, n) chromosome number and are referred to as *euploids*.

Sorghum halepense, a common weed sometimes used as a forage grass, and *Sorghum almum*, also used as a forage grass, are primarily *autotetraploid*, having 4n, or 40, chromosomes. The chromosome number can be doubled by using colchocine, and some effort has been made to breed tetraploid grain sorghums.

Aneuploids

Aneuploids may occur in a number of forms; i.e., *monosomic* in which one chromosome is absent (2 n - 1) and *trisomic* in which there is an extra chromosome (2n + 1). In many cases aneuploidy causes reduced vigor, and such plants are usually very different in appearance from the normal diploid plants. Aneuploidy may even result in the death of the plant, particularly in diploid species.

Aneuploids provide a useful tool for the study of the genetics of various characters. Use of aneuploids often permits determination of the location of genes on particular chromosomes.

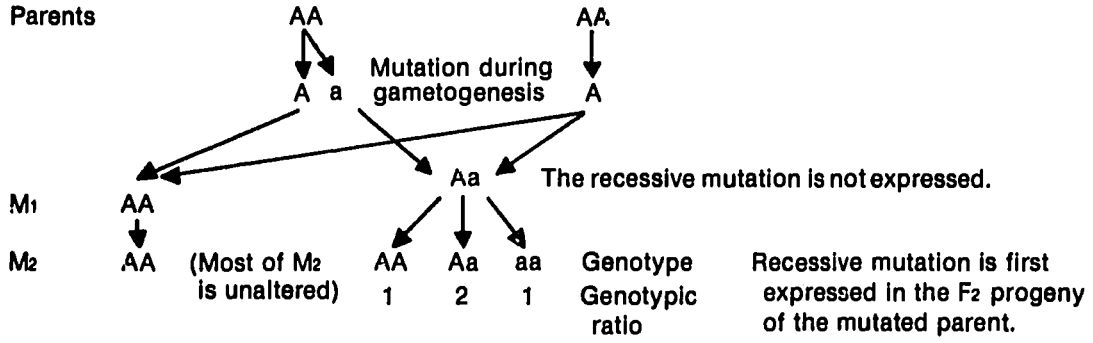


Figure 3.19: The generations following a mutation.

Euploids

An estimated one-third of all domesticated species of plants (and over 70% of forage grasses) are euploids, with multiples of either the basic or the genome number of chromosomes. There are two main types of euploids, autopolyploids and allopolyploids, depending on the origin of the chromosomes (Fig. 3.20).

Autopolyploids occur when the same *genome*—the complete set of chromosomes in a given species—is duplicated. Thus if the genome number (n) for a given species is six chromosomes, then the normal diploid plant will have two sets of these six chromosomes, or 2n = 12. The autotriploid plant will have three sets, 3n = 18; the autotetraploid four sets, 4n = 36, etc.

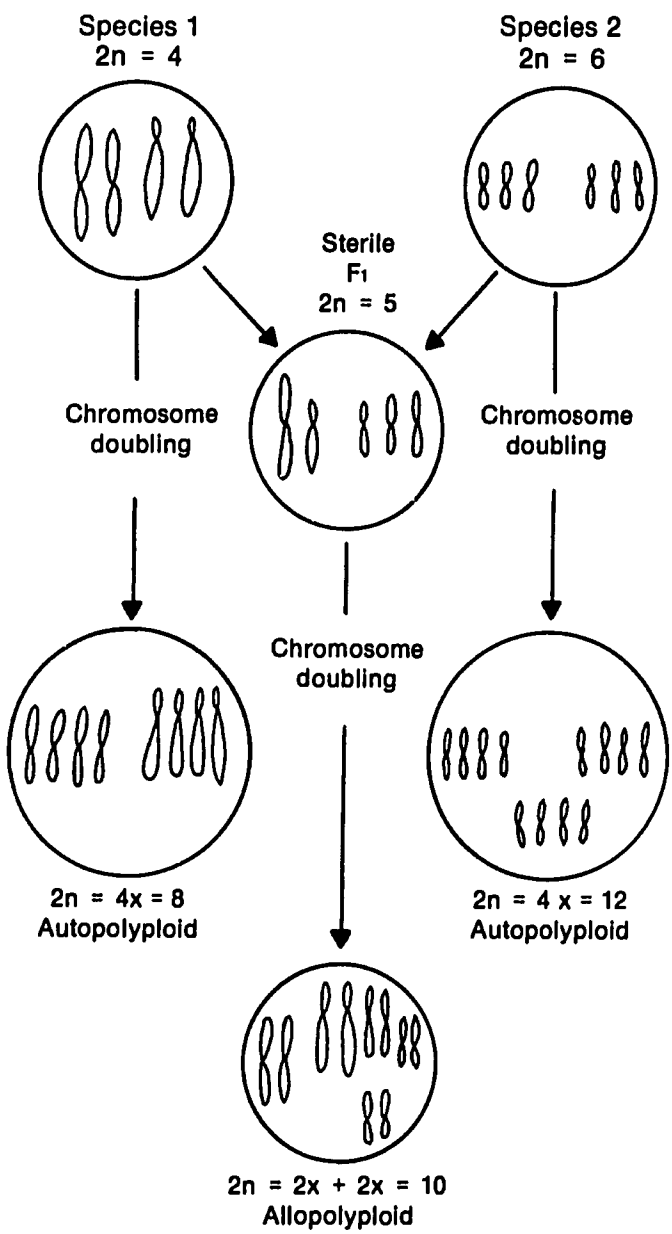


Figure 3.20: The origin of autopolyploids and allopolyploids.

Autopolyploids usually have larger cells and often have larger flowers, fruits, and leaves than diploids, but they normally have reduced fertility. The reduction in fertility is due mainly to the behavior of the chromosomes at meiosis. In the diploid, each chromosome has a counterpart, and together they form a homologous pair of chromosomes. In a tetraploid there are four homologous chromosomes. Instead of normal bivalent formation during meiosis, these four chromosomes may form a *quadrivalent* (i.e., all four chromosomes may come together) or a trivalent plus a univalent (three chromosomes join and one remains alone). When the chromosomes separate and move to opposite ends of the cell during anaphase 1, all four chromosomes may go to one end, or three may go to one end and one to the other. If either of these events occurs, the gamete is likely to be nonfunctional; i.e., it is unable to combine and form offspring in a normal way.

In many crop species, this reduced fertility may not be a problem if they can be reproduced asexually; e.g., through the formation of tubers (potatoes) or by grafting (apples and pears).

Allopolyploids are the result of hybridization between two separate species, usually followed by a doubling of the chromosome number. When two species are crossed, the F_1 generation is usually sterile because pairing cannot take place between chromosomes from different genomes. If the species are very close, the genomes may be similar and some pairing may occur, but in general very few, if any, fertile gametes will be produced (Fig. 3.20). If the chromosome number is doubled, however, normal pairing will result between homologous chromosomes. In an allotetraploid there are two sets of each genome, and fertility is frequently very high. Many important crop species are allopolyploids, including bread wheat (a hexaploid species).

Euploids may arise in two ways:

1. During mitosis in normal diploid plant cells (*somatic cells*), both sets of chromatids may be combined in a single nucleus, resulting in a doubling of the chromosomes. If new cells are formed from this cell, they also will have 4n chromosomes. If such cells are present in the flowers as *pollen mother cells* and *embryo-sac mother cells*, the gametes will have 2n chromosomes; on fertili-

zation they will produce autotetraploid plants in the next generation.

2. Chromosome doubling may occur during meiosis. The chromosomes may fail to separate during anaphase and both may pass to one pole of the cell, resulting in a 2n gamete. If a gamete with 2n chromosomes unites with a gamete with n chromosomes, an autotriploid (3n) plant will be produced. Polyploids with an odd number of genomes are usually completely sterile, because normal pairing of homologous chromosomes cannot take place.

Inheritance in Polyploids

The inheritance of characters in polyploid species differs from that in diploids in several respects. Allotetraploids generally behave as diploids, especially if the two genomes are very different. In autotetraploids, however, up to four alleles can be present at a particular locus, instead of two in the diploid. If there is no interaction between the alleles, many new phenotypes can be produced that are not possible in the diploid.

Consider the series of alleles A_1, A_2, A_3, and A_4. Any two of these four can be present in a diploid plant, but all four can be present in a tetraploid.

An autotetraploid that has the genotype $A_1 A_2 A_3 A_4$ will have six possible types of gametes (A_1A_2, A_1A_3, A_1A_4, A_2A_3, A_2A_4, A_3A_4), and all six will be found in essentially equal proportions.

If there are only two alleles, there are five possible genotypes in a tetraploid ($A_1A_1A_1A_1$; $A_1A_1A_1A_2$; $A_1A_1A_2A_2$; $A_1A_2A_2A_2$; and $A_2A_2A_2A_2$), as compared with the three genotypes (A_1A_1, A_1A_2, and A_2A_2) in a diploid.

In diploid plants, the number of possible genotypes is given by 3^n, where (n) is the number of loci, assuming that there are only two possible alleles at each locus. Thus, in the diploid that has five such loci, there are $3^5 = 243$ genotypes. In tetraploids, the number of possible genotypes (again assuming there are only two alleles) is given by 5^n. Thus, in the tetraploid, there are 5^5 genotypes = 3125, if five loci are involved.

Quantitative Inheritance

The characters discussed so far can be classified into a few distinct classes: green or yellow; tall or short; red, pink, or white, etc. Many characters cannot be classified in this way, however, because classes are not so readily separated—the observed variation is *continuous*. Characters that exhibit continuous variation are called *quantitative characters*, and most of the economically important characters in plants (height, maturity, yield, etc.) are quantitative.

The study of the inheritance of quantitative characters depends on measurements of plants, rows, or plots. Graphs can be drawn to show the variation, and it can be described mathematically by the *mean* (the average value of a population) and the *standard deviation*, or variance, which gives a measure of the spread of the values on either side of the mean.

Continuous variation in a character is the result of:

1. control by genes at many loci, or
2. considerable influence by the environment. Both the genotype and the environment are important in the expression of most quantitative characters.

Variation Due to Environment

Almost all quantitative characters are influenced by the environment to a great extent. In terms of the formulas discussed at the beginning of this section, V_E is normally high. Even characters that are controlled by alleles at a single locus can appear to be quantitative in nature if the influence of the environment is sufficiently large. The effect of the environment on a character controlled by a single gene pair (hypocotyl length) is shown in Figure 3.21. The graphs for the F_1 and F_2 generations show that this character is controlled by a single gene, with long hypocotyl (AA) being dominant to short (aa), but the strong environmental influence has caused the separate classes to overlap and an analysis based on the numbers of plants in each class is impossible.

Plant height may be a quantitative character; however, in Mendel's experiment of tall x short plants, the mean height of the tall plants was about 200 cm, while the mean of the short plants was only about 30 cm. Thus, even if there were large environmental variation, the plants could be classified easily into separate classes. In sorghum, four loci are known to be involved in the control of plant height.

Variation Due to Genotype

Not all quantitative effects can be explained by environmental influences, and it is now known that many quantitative characters are controlled by a large number of genes at many different loci. In this situation, segregation in the F_2 population does not form discrete classes, and generally there is a con-

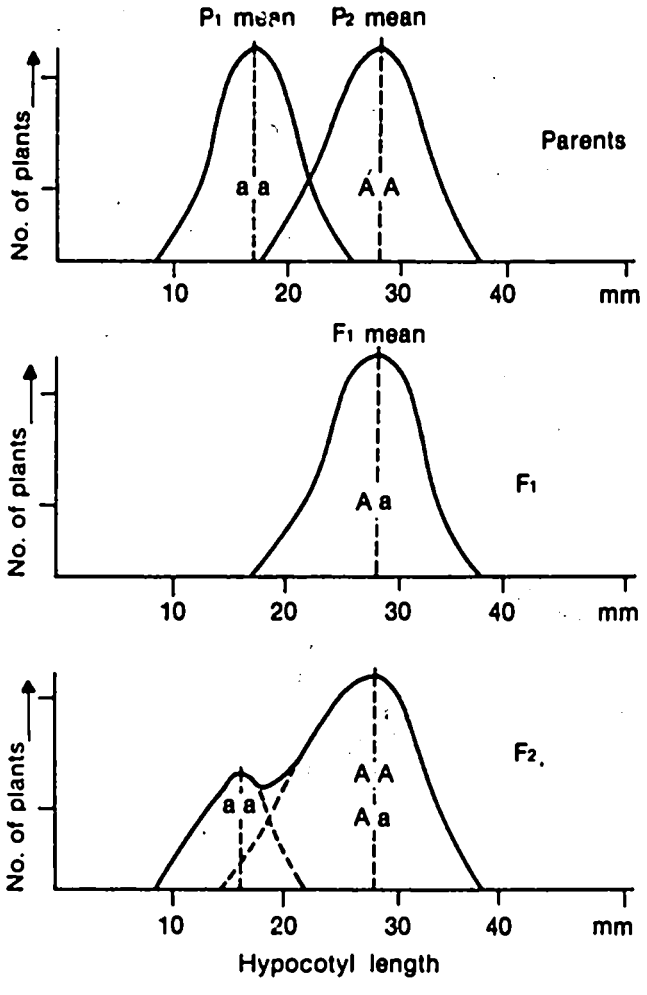


Figure 3.21: Graphs showing a cross involving a single locus with strong environmental influence.

tinuous distribution between parental values without the bimodal (having two peaks) curve shown in Figure 3.21. This form of inheritance, shown in Figure 3.22, is known as *polygenic inheritance* (poly = many).

The mean of the F_1 generation is generally intermediate between the parental means, and plants in the F_2 can usually be found covering the whole range of parental values.

The basis of polygenic inheritance can be explained on the assumption that many genes are involved in determining such characters, that they frequently lack dominance, and that their action is additive. The genes, however, are inherited in ways identical to those discussed previously.

The data of Nilsson-Ehle, a Swedish geneticist, fit well with this explanation, although genes at only two loci were found to be involved. He crossed two wheat varieties: one with deep red grain and the other having white grain. He found that the F_1 generation was medium red. In the F_2, $^1/_{16}$th of the plants had deep red grain, $^1/_{16}$th had white grain, and the rest were intermediate. On further analysis of the intermediate grains, it was found that $^6/_{16}$ths were medium red like the F_1; $^4/_{16}$ths were darker than the F_1 but lighter than the deep red parent; and $^4/_{16}$ths were lighter than the F_1 but were not white. This finding can be explained by assuming that the deep red color is due to the genotype $R_1R_1R_2R_2$; that white is due to $r_1r_1r_2r_2$, that the genes lack dominance, and that their action is additive. The F_1 has the genotype $R_1r_1R_2r_2$ and is intermediate between the two parents because it has two color genes (R_1 and R_2). In the F_2, other shades of red are produced by genotypes with one or three color genes. This is shown in Figure 3.23.

This type of inheritance has resulted in a 1:4:6:4:1 ratio and has been produced by genes at only two

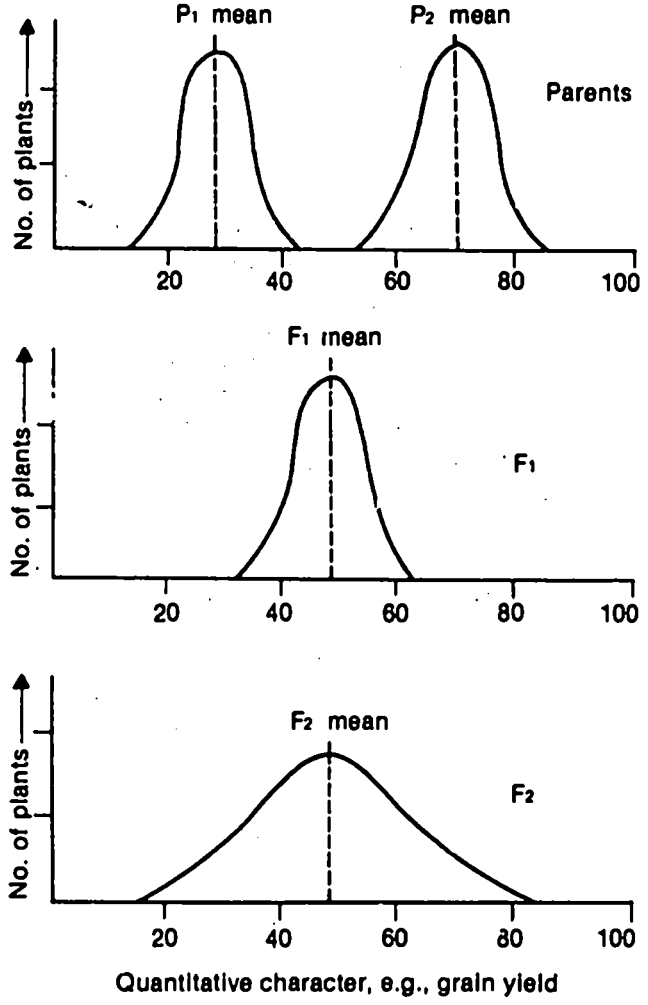


Figure 3.22: The inheritance of a character controlled by many genes.

Parent	Deep red $R_1R_1R_2R_2$	×		White $r_1r_1r_2r_2$	
F_1		Medium red $R_1r_1R_2r_2$			
F_2	Genotype	Genotypic ratio	Phenotype	No.of color genes (R)	Phenotypic ratio
	$R_1R_1R_2R_2$	1	Deep red	4	1
	$R_1R_1R_2r_2$ $R_1r_1R_2R_2$	2 2	Red	3	4
	$R_1r_1R_2r_2$ $R_1R_1r_2r_2$ $r_1r_1R_2R_2$	4 1 1	Medium red	2	6
	$R_1r_1r_2r_2$ $r_1r_1R_2r_2$	2 2	Light red	1	4
	$r_1r_1r_2r_2$	1	White	0	1

Figure 3.23: The inheritance of grain color in wheat, based on the findings of Nilsson-Ehle.

loci (R_1 and R_2). The grain color character is virtually unaffected by the environment, and the F_2 can be divided into separate classes. If the environment had produced a small effect, the classes would overlap and true continuous variation would have occurred (Fig. 3.24).

Most polygenic characters are controlled by genes at many loci, and the number of possible genotypes is very large. If only two loci are involved, there are nine possible genotypes (assuming only two alleles are possible at each locus). If three loci are involved, there are 27 genotypes; and if four are involved, there are 81 possible genotypes. If n = the number of loci (each with only two alleles), the number of genotypes in the F_2 is 3^n. Thus if 10 loci are involved, there are 3^{10} genotypes = 59 049; and if 13 loci are involved, there are over 1.5 million possible genotypes in the F_2 generation. Many important characters, such as yield, may be influenced by genes at tens or even possibly hundreds of loci, and the number of genotypes is enormous.

Additive, Dominance, and Epistatic Gene Action

The above explanation of polygenic inheritance is based on the assumption that (1) there is no dominance of one allele over another at a given locus, and (2) the effects of all the genes at all the loci are additive; i.e., as the number of alleles for the trait increases, the expression of the trait increases proportionately.

In practice, in addition to the additive effects of the genes, both dominance and interactions between genes at different loci (epistasis) may be important in the inheritance of quantitative characters.

The effect of the genes showing dominance or epistasis will cause the distribution in the F_2 population to be skewed; i.e., it will not be symmetrical on either side of the mean (Fig. 3.25).

Statistically, dominance and epistasis can be expressed as components of genetic variance $V_G = V_A + V_D + V_N$,

where V_A = the variance due to the additive effects of the genes,
V_D = the variance due to the dominance effects of the genes,
V_N = the variance due to the nonallelic (epistatic) effects of the genes.

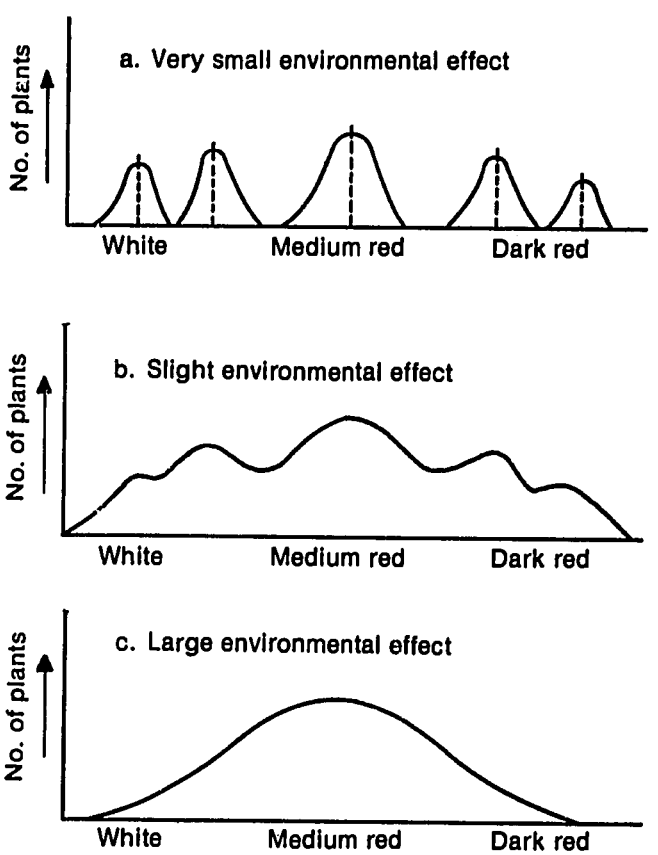


Figure 3.24: The effect of environment on a polygenic character controlled by only two genes.

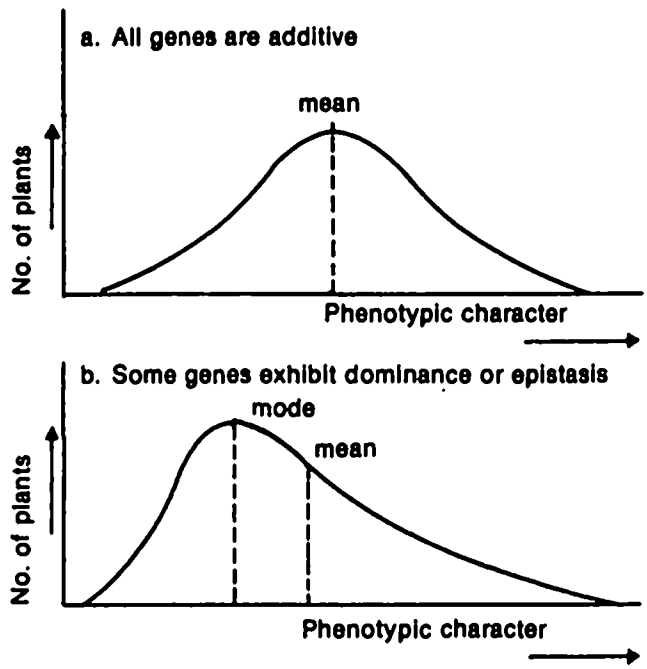


Figure 3.25: Effect of dominance on quantitative traits.

Since $V_P = V_G + V_E$ (where V_E = environmental variance), the total phenotypic variance V_P can be divided into four components:

$$V_P = V_A + V_D + V_N + V_E$$

In the absence of dominance and epistasis, genetic variance $V_G = V_A$.

Additive genetic variance (V_A) is the chief cause of resemblance among parents and offspring, and it is frequently greater than the combined dominance and epistatic variances.

Especially designed experiments must be conducted to calculate these components, usually requiring analysis of the parents, F_1, F_2, and backcross generations. (A technique known as the diallel cross analysis is commonly used to determine the variance components, but this will not be discussed here.)

Population Genetics: Gene Frequency and Equilibrium

Two basic concepts that plant breeders should understand are segregation in the Mendelian sense and changes in gene frequencies in populations.

Thus far, genetics has been discussed in relation to segregation ratios produced by the progeny obtained from crosses between specific plants. However, the breeder usually deals with genetic phenomena in groups of individuals or populations that show no apparent Mendelian segregation ratios, but which follow the laws of Mendel.

The population, in the genetic sense, is more than a group of individuals; it is a breeding group. Population genetics is concerned with both the genetic composition of the population and the transmission of genetic material to the next generation. In every generation, the genetic composition of the individual breaks apart and reappears in a new form in the next generation. The genes carried by the population have continuity from generation to generation, but there is no such continuity in the genotypes in which the genes appear. The genetic constitution of the population is described by an array of gene frequencies (Falconer 1964).

For the breeder, differences in populations are usually of degree rather than of kind. Mendel was able to work with counted ratios in progeny, and the Chi-square test could be used to check *observed* against *expected* ratios. However, population genetics works with natural or controlled populations to observe phenomena and attempt to describe them with mathematical models. These mathematical models cannot reflect all the complexities of the population in its environment. Thus it is always necessary to make assumptions for which the mathematical models are relevant. The conclusions are always restricted in their interpretation by these assumptions. However, the concepts (models) developed have proven useful in describing phenomena in populations; these are of fundamental importance and should be well understood by the breeder as he sets up his crop-improvement program (Crow and Kimura 1970).

Gene Frequency

A basic concept in population genetics is that of *gene frequency*. To understand this concept, consider the following:

- Assume two alleles (Aa) at one locus.
- Assume a population of N diploid individuals.
- Let D equal the number or proportion of dominant individuals (AA); H the number or proportion of heterozygous individuals (Aa); and Q the number or proportion of recessive individuals (aa). Then D, H, and Q are genotypic proportions or frequencies in the population.

Note that although there are three types of individuals in this population, AA, Aa, and aa, there are only two kinds of alleles, A and a. These N individu-

als have 2N alleles (individuals in the population are diploid 2n). Each AA individual has two A alleles, and each Aa individual has one A allele; therefore the total number of A alleles in the population is 2D + H and the proportion of allele A in the population is:

$$\frac{2D + H}{(2N)} \quad \text{or} \quad \frac{D + \frac{1}{2} H}{(N)}$$

This proportion is the frequency of allele A in the population and is denoted by the letter "p." The frequency of allele "a" is denoted by "q" and is calculated in the same way:

$$q = \frac{(H + 2Q)}{2N} = \frac{(\frac{1}{2}H + Q)}{N}$$

Note that p + q = 1, so that p = 1 - q. The frequencies of genotypes AA, Aa, and aa are given as percentages rather than actual counts; for example, 2, 12, 26 would become 0.05, 0.30, and 0.65, and p would equal:

$$\frac{D + \frac{1}{2}H}{N} = \frac{2 + 6}{40} = \frac{8}{40} = 0.2,$$

$$\text{and } q = 1 - p = 1 - 0.2 = 0.8.$$

To grasp the concept of gene frequency in a population, the following example should help (Falconer 1964). The MN blood group in man has been thoroughly studied: M and N are two alleles at the same locus, and a cross of MM x NN individuals would result in an MN F_1. The mating between two MN parents would result in an expected ratio in F_2 progeny of MM:2MN:NN in accordance with Mendelian segregation. This expected ratio would occur no matter where the parents lived. However, sampling of the populations in Greenland and Iceland produces the following results:

	Blood Group (Frequency, %)			Number of
	MM	MN	NN	individuals
Greenland	83.5	15.6	0.9	569
Iceland	31.2	51.5	17.3	747

It is obvious that the genotypic frequencies in these two populations differ, the NN group being much more common in Iceland than in Greenland. (Remember that in both locations an F_2 ratio of MM:2MN:NN would be expected in the offspring resulting from an MN x MN mating.) These populations differ in both their genotypic and gene frequencies, yet the laws of Mendel apply equally to both.

The frequency of alleles (p,q) for a particular locus can be obtained from the genotypic frequencies (D, H, Q). Consider the following example involving the MN blood groups:

$$M = D + \tfrac{1}{2}H = 0.835 + \frac{0.156}{2} = 0.835 + 0.078 = 0.913$$

$$N = Q + \tfrac{1}{2}H = 0.009 + \frac{0.156}{2} = 0.009 = 0.078 = 0\ 087$$

The frequencies of alleles for the MN blood groups in Greenland and Iceland then are:

	Allele M	Allele N
Greenland	0.913	0.087
Iceland	0.57	0.43

These differences in frequencies are substantial.

This example indicates what genotype and gene frequencies are, and how they differ from Mendelian segregation ratios between selected parents. A working knowledge of these concepts is a requisite to understanding the various procedures undertaken in a breeding program.

The Hardy-Weinberg Law

A basic principle in population genetics was independently discovered by Hardy and Weinberg in 1908. They found that in a *random-mating population* (i.e., a population in which each male gamete has an equal chance of mating with any female gamete), and in the absence of any disturbing factors (selection pressure, mutations, etc.), the relative frequency of a gene remains constant generation after generation. The proportion of different genotypes also remains constant after equilibrium has been reached following one generation of random mating.

This can be illustrated as follows:

Let the frequency of allele A = p and the frequency of allele a = q. The gametes containing the A and a alleles will be produced in the same relative frequencies: p and q, respectively. If the union of these gametes is entirely random, then the following combinations will be produced.

		Female gametes	
		A p	a q
Male gametes	A p	AA p^2	Aa pq
	a q	Aa pq	aa q^2

Thus, in the next generation, the frequency of genotype AA will be p^2, the frequency of genotype Aa will be 2 pq, and the frequency of genotype aa will be q^2.

As an example of how this works, consider a population of 100 plants consisting of 20 plants with the genotype AA, 20 with Aa, and 60 with aa. In such a population, the frequency of the A allele is 0.3—i.e., $p = (D + \frac{1}{2}H)/N$. That is, 30% of all the alleles in the population at the A locus are A, and the frequency of allele a is (1-p), or 0.7 (i.e., 70% of all the alleles in the population at the A locus are a).

Thus, p = 0.3 and q = 0.7.

In the generation arising from this cross, the genotypes will be found in the following frequencies:

AA	=	p^2	=	0.3 x 0.3	=	0.09
Aa	=	2pq	=	2 x 0.3 x 0.7	=	0.42
aa	=	q^2	=	0.7 x 0.7	=	0.49
				Total	=	1.00

Thus, if the population still comprises 100 plants, there will be about nine plants with genotype AA, 42 plants with genotype Aa, and 49 plants with genotype aa.

In this new population, the number of A alleles is 18 (from genotype AA) + 42 (from genotype Aa) = 60 out of a total of 200 alleles. The frequency of allele A is thus 0.3. The frequency of "a" can be worked out in the same way, and is found to be 0.7.

Thus, the frequencies of the alleles A = p = 0.3 and a = q = 0.7 have remained constant from the original population. In the original population, the genotypic frequencies were AA = 0.2, Aa = 0.2, and aa = 0.6. After one generation of random mating, the genotypic frequencies were found to be AA = 0.09, Aa = 0.42, and aa = 0.49.

From this generation onward, both the genotype and gene frequencies will remain unaltered providing the following conditions are upheld:

- Mating occurs entirely at random in very large diploid populations.
- Allele A and allele a are equally fit; i.e., there is no advantage to the plant in having A rather than a, or vice versa. If one allele confirms a more superior trait than the other, then selection pressure (either natural selection or artificial selection by a breeder) will favor one allele and will act against the other.
- There is no differential migration of one allele into or out of the population.
- The mutation rate of allele A to a is the same as the mutation rate of allele a to A.

When the population is not in equilibrium, the frequencies of p and q are found from the formulas $p = (D + \frac{1}{2}H)/N$. However, when the populations are in Hardy-Weinberg equilibrium, the frequencies of p and q equal the square root of the frequency of the homozygous type for that gene. Using the above example, the frequency of allele A from the original population is determined to be $p = (D + \frac{1}{2}H)/N$ or $(20 + \frac{1}{2}[20])/100 = 0.3$ after one generation of random mating. The genotype frequency of the AA homozygote is 0.09, and the square root of 0.09 is 0.3. The formula $p = D + \frac{1}{2}H$ still holds; i.e., $p = 0.09 + \frac{1}{2}(0.42) = 0.09 + 0.21 = 0.3$.

In a random-mating population, the variability does not change from generation to generation (Crow and Kimura 1970).

The maximum frequency of the heterozygous portion of the population (H) can never exceed 0.5, and this occurs when p = q = 0.5. H can be greater than D or Q, but never greater than D x Q.

Another property of an equilibrium population is that the proportion (or number) of heterozygotes is twice the square root of the product of the two homozygous proportions (or number); i.e.

$$\frac{H}{\sqrt{D + R}} = 2.$$

This property offers a simple test for equilibrium—a test having the advantage that the ratio 2 is independent of the gene frequencies of the population.

Note if D=0.10, H=0.20, and R=0.70 that

$$\frac{H}{\sqrt{D+R}} = \frac{0.20}{\sqrt{0.10 \times 0.70}} = \frac{2}{0.265} \neq 2 \text{ but that}$$

$$\frac{0.32}{\sqrt{0.40 \times 0.64}} = \frac{0.32}{\sqrt{0.0256}} = \frac{0.32}{0.16} = 2$$

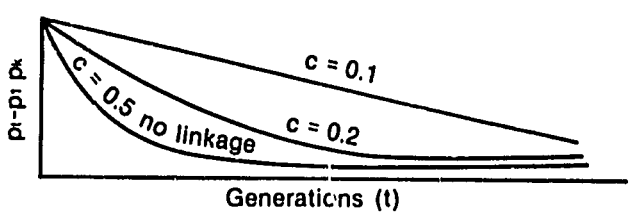
using the frequencies before and after equilibrium is attained.

Note:
$p = 0.1 + 0.1 = 0.2$
$q = 1 - p = 0.8$
$D = p^2 = (0.2)(0.2) = 0.04$
$H = 2pq = 2(0.2)(0.8) = 0.32$
$R = q^2 = (0.8)(0.8) = 0.64$

Although the Hardy-Weinberg law rests on assumptions of a large random-mating population free of pressures such as mutation and selection, it

has been found that the law is approximately true for a great majority of genes in most cross-fertilizing species (Crow and Kimura 1970). Departures occur mostly because of inbreeding and assortative mating. Inbreeding is extreme in self-fertilizing species, but can occur in cross-pollinated species closely spaced in a field, or geographically. Assortative mating takes place in situations where crossing would tend to occur more often between some types than between others. For example, in a sorghum composite, early flowering types would tend to cross together and late types would tend to cross together, simply because of flowering time.

Involvement of More Than One Locus: The Hardy-Weinberg law states that equilibrium is established at any locus after one generation of random mating. It is possible for the alleles at two loci to be in random-mating frequencies and yet not in equilibrium with respect to each other (Crow and Kimura 1970). In fact, equilibrium between two loci is not obtained after one generation of random mating, but is obtained slowly over many generations. The effect of linkage is to slow down the rate—the closer the linkage the slower the rate.



The above graph shows the approach to genetic phase or linkage equilibrium. The ordinate (y axis) is the difference in frequency of the genotype at any particular time and the equilibrium frequency, $p_i - p_i p_k$. The value of "c" gives the linkage frequency between two loci.

The equilibrium value is approached slowly, and (theoretically) is never attained. In the case of no linkage (c = 0.5), the difference between the actual gene frequency and the equilibrium value is reduced by one-half in each generation, and about seven generations are required to reach approximate equilibrium. About 69 generations are required for c to equal 0.01, and about 693 generations are required for c to equal 0.001.

The composite gene frequency of two loci can be found by multiplying together the individual gene frequencies. For example, if the frequency at the Aa locus is 0.3 and at the bb locus is 0.65, the composite frequency of the genotype Aabb would be 0.3 x 0.65 = 0.195.

Crosses Between Populations of Different Gene Frequencies: The question sometimes arises as to what happens when two populations are crossed; particularly if, for example, an agronomically poor source of insect tolerance is to be crossed with an agronomically elite susceptible type. What happens to the gene frequency for insect resistance?

Consider two populations where p_1 and p_2 represent the frequencies for allele A; then the gene frequency in the F_1 generation is the mean of the two parent population frequencies, or $p = (p_1 + p_2)/2$. If the frequency for a resistance factor in the source material is p = 0.8 and in the agronomically elite material is p_2 = 0.04, then the gene frequency in progeny of the cross between them would be $p = (p_1 + p_2)/2 = (0.8 + 0.04)/2 = 0.42$. The gene frequency for the resistance trait is reduced by approximately half.

Hybridization between two populations results in an initial decrease in homozygosity, followed by a rise in frequency to a point halfway between the parent populations. The effect of linkage is to slow the rate of progress toward equilibrium (Mather 1963).

Factors That Change Gene Frequency

There are two major types of processes that change gene frequencies: a *systematic process* that is predictable in both the direction and the amount of change, and a *dispersive process* that is unique to small populations and is predictable in amount, but not in direction. The systematic processes are selection, migration, and mutation (Falconer 1964). The following example demonstrates these processes:

The sorghum variety Shenoli is susceptible to a fungus disease called downy mildew. Assume that in India this disease is very severe around Sangli, less severe around Dharwar, and not often found at Coimbatore. Most of the collection observed at Dharwar is free from the disease, which suggests that sensitivity may be recessive in nature and under the control of relatively few genes. For the sake of discussion, it will be assumed that susceptibility is controlled by the single recessive allele dm, so that DmDm and Dmdm plants are equally resistant. (This symbolism and the genetic assumption are hypothetical.)

If a cross is made between a DmDm and a dmdm plant, the F_1 generation (Dmdm) will be resistant. In 1000 F_2 plants the expected frequency of resistant

plants would be ¾ (750 individuals of either DmDm or Dmdm genotype), and the expected frequency of susceptible plants would be ¼ (250 individuals of dmdm genotype). An observed ratio of 730 to 270 would satisfy this expected ratio.

In these 1000 individuals, half the gametes will be Dm: i.e., two gametes from the homozygous dominant parent and two from the heterozygous parent, or AA + 2 Aa; and half the gametes will be dm; i.e., two gametes from the recessive parent and two from the heterozygote. In terms of population genetics, the gene frequency of dm (denoted as q) will be one-half, and the gene frequency of Dm (denoted as p) will also be one-half.

If a large planting is made at Coimbatore from this F_2 population and open pollination is allowed, the gene frequency will not change. (For the sake of argument assume that downy mildew does not occur at Coimbatore: there is no selection pressure against the recessive allele, because the pathogenic organism is not there.) This can be demonstrated in the following way:

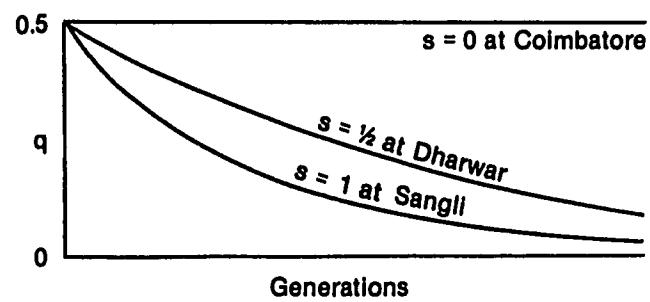
		Female gametes	
		0.5 Dm	0.5 dm
Male gametes	0.5 Dm	DmDm 0.25	Dmdm 0.25
	0.5 dm	Dmdm 0.25	dmdm 0.25

DmDm (0.25) + 2 Dmdm (0.50) = ¾
dmdm (0.25) = ¼

This is the same frequency obtained before, under conditions of random mating. In the absence of any factors that tend to change gene frequency, the gene frequency of this population will remain p = 0.5 and q = 0.5. This principle was discussed under the Hardy-Weinberg law (p.53 ff.)

Suppose that this same F_2 population was also planted at Dharwar and at Sangli. Plants severely infected with downy mildew will not reproduce (assume that none of them do). Assume that at Sangli all susceptible plants succumb to the disease, while at Dharwar only half of them do (the selection pressure, denoted as "s," will then be equal to 1 at Sangli and to ½ at Dharwar). When this population of 1000 F_2 individuals is planted at Sangli, only the 730 resistant plants will produce seed; the other 270 will fail to produce seed because they are diseased. The reproducing population then is DmDm : 2 Dmdm, and the gametes in the population will be 4 Dm : 2 dm; that is, $^4/_6 = ^2/_3$ will be Dm, and $^2/_6 = ^1/_3$ will be dm ($p = ^2/_3$; $q = ^1/_3$). Therefore, at Sangli, after one generation the frequency of Dm has changed from p = ½ to $p = ^2/_3$. This change in gene frequency will be rapid at first, but will decline, so that many generations will be required before the recessive trait will disappear. Actually, the dm allele will never disappear completely from the population, because the Dm allele mutates to dm with some frequency (population geneticists frequently denote this as μ). In this case, then, the gene frequency (instead of being at equilibrium p = q = 0.5 as at Coimbatore) will come to equilibrium at some low value of q where the loss in the dm allele due to selection is balanced by the mutation frequency of Dm to dm. (An expanded discussion of this is presented later in this section.)

At Dharwar, only half of the dmdm plants in the F_2 population will produce seed. The zygotic proportion of seed-producing plants is, therefore, 1 DmDm : 2 Dmdm : ½ dmdm, or 2 DmDm : 4 Dmdm : dmdm. The number of Dm gametes will be 4 + 4 = 8 and dm gametes will be 4 + 2 = 6. The frequency of Dm will be $^8/_{14}$ (0.57), which is greater than ½ (0.50), but less than $^2/_3$ (0.66), where s = 0 and s = 1, respectively. The frequency of dm will be $^6/_{14}$ (0.43), which is less than q = 0.5 (s = 0), but greater than q = 0.33 (s = 1). The same equilibrium point will be reached as in the previous case, but it will take much longer. The change in the gene frequency (Δq) of q is demonstrated by the following:



This is a very approximate figure; many generations can be involved.

Suppose that every year some of the seeds of this crop had to be purchased from Coimbatore (say 10%) and that these seeds were mixed equally with the other seeds produced in the Sangli area. In this 10%, ¼ of the plants will be DmDm, ½ will be Dmdm, and ¼ will be dmdm. Therefore, $^1/_{40}$th, or 2.5%, of the plants in the farmers' fields would be susceptible and would not produce seed. Also of this 10%, half would be heterozygous for the factor Dmdm, so the frequency of q would increase by 2½%. The population geneticist terms this change in gene frequency *migration*. If the frequency of q is in equilibrium

between selection and mutation pressures, migration (tending to increase q) will act in the same direction as mutation, and a new equilibrium value will be attained at a higher value of q. Again, this is very approximate, because it would take many generations to change from one frequency to another, and it is not likely that the rate of migration would remain constant for so long. (Actually, if the plant breeder and pathologist were working effectively, they would probably try to prevent the sale and transport to Sangli of seed grown in the Coimbatore area.)

If the plant breeder released a variety resistant to downy mildew, the use of seed from this original F_2 population might almost disappear in the Sangli area. A few cultivators might still persist in growing a small plot in a kitchen garden for some special purpose. Under this circumstance, the gene frequency q may change from generation to generation due to chance combination. This chance variation in q one way or the other may be much greater than the influence of selection, migration, or mutation. However, such chance variation is important only when the population size is very small. It is also possible, due solely to chance, that the gene frequency (q) will reach 0 after relatively few generations in a small population. The most important practical application of this to the plant breeder would be in maintaining the dm allele in the population for purposes of collection. Some pathologist in future years might have real need for dmdm plants, and if the plant breeder has not maintained a sufficiently large population in his collection, this allele may be permanently lost.

The following section will present an expanded discussion of what has been said here and will consider a wider range of possibilities. A basic point to remember is that—whether q = 0.5, 0.05, or 0.0005—any time an F_2 population is obtained from a DmDm x dmdm cross the expected progeny ratio will be ¾ Dm- to ¼ dmdm.

Selection

For the plant breeder, selection is probably the most important force available for changing gene frequency. The aim of selection is to produce a population that has a mean value greater (or less) than the mean value of the parent population. This difference should be due to differences in genotype and not due to the environment. In selecting for yield, for example, the mean yield of the progeny of the selected plants should be greater than the mean yield of the population from which the plants were selected. The selected population can be a bulk of the selected plants, or the progeny of each selected plant can be grown separately and the advance can be measured by the mean performance of the lines.

If selection is to be effective, two conditions must be met:

- There must be phenotypic variation for the selected character.
- At least part of this variation must be genetic.

If the first condition is not met, selection will not be possible—since there would be no observed differences between the parents.

If the observed phenotypic variation is entirely due to environmental (nonheritable) variation, the progeny of the selected plants will not be genetically different from the parents and no genetic advance can be made.

To illustrate this point, consider the following examples by Johannsen (1903). From a mixture of homozygous lines of beans, he selected a number of seeds on the basis of their size. He found that the progeny of the large seeds were large, the progeny of the medium seeds were medium, and the progeny of the small seeds were small. The progeny of each selection showed variation, but considerably less than in the original population, and he found that further selection was of no use. In the original population, there was both genetic and environmental variation; but after selection, the remaining variation was due to the environment. Figure 3.26 shows what would occur if four homozygous lines were present in the original population: AABB, AAbb, aaBB, and aabb. It can be seen that selection would be effective only if genetic variation were present and that selection in a *pure line* (a population of identical homozygous plants) would not be useful.

In practice, breeders usually make selections in segregating populations following a cross (F_2, F_3, F_4, etc.). In this case the selected plants will not be homozygous for all loci, and selection may be effective for several generations—until near homozygosity is reached.

Heritability: The observed phenotypic variance (V_P) is made up of the genetic variation (V_G) plus the environmental variation (V_E). If selection is to be effective, V_G should be large and V_E should be small. The proportion of the total variance that is genetic is called the *heritability* (H). It is usually expressed as a percentage, thus:

$$H = \frac{V_G}{V_P} \times 100$$

$$\text{or } H = \frac{V_G}{V_G + V_E} \times 100$$

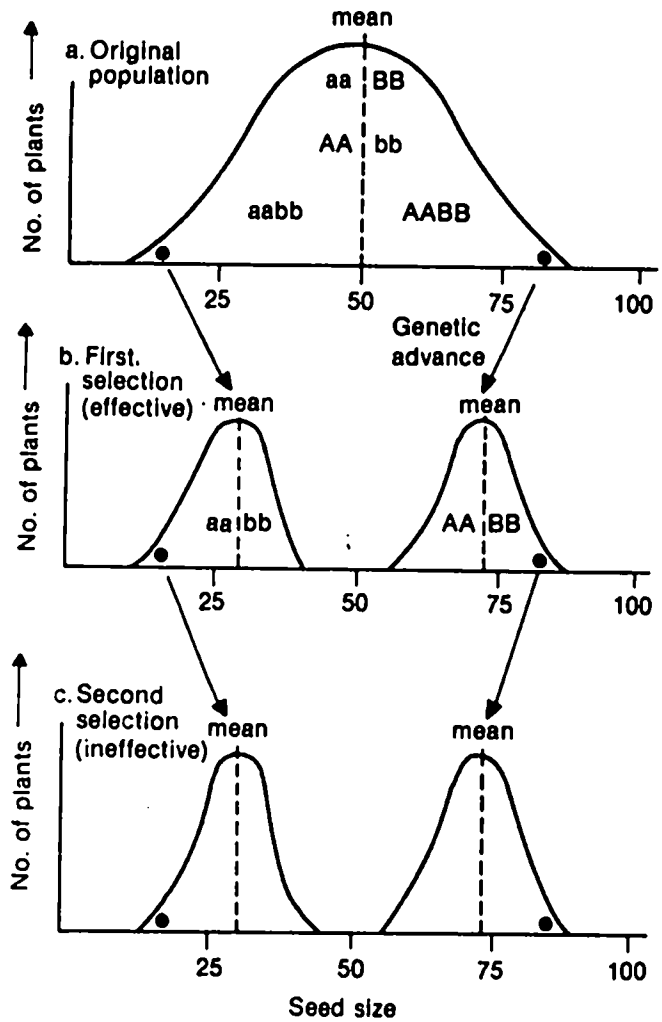


Figure 3.26: Selection in a mixture of pure lines.

Sometimes only the additive genetic variance (V_A) is used in estimates of heritability, since this is the most important component of genetic variance. In this case:

$$H = \frac{V_A}{V_P} \times 100$$

$$\text{or } H = \frac{V_A}{V_A + V_D + V_N + V_E} \times 100$$

This form of heritability is sometimes called *narrow-sense heritability*, and that which takes into account the total genetic variance is called *broad-sense heritability*. If the heritability is high, it means that the genotype plays a more important role than the environment in determining the phenotype. A character with high heritability is thus more likely to respond to selection than a character with low heritability. In general, characters controlled by only a few genes have higher heritability than polygenic characters such as yield, maturity, harvest index, etc.

Genetic Advance Due to Selection: The advance in the mean value of a population as a result of selection will depend on three things:

- heritability of the character concerned,
- total variation in the population from which to select, measured as V_P, and
- selection pressure (i.e., the proportion of the population that is selected).

The phenotypic variance, V_P, is important, since if there is only a small degree of variation in the population, there will not be a very wide range from which to select (Fig. 3.27). Even if the heritability is 100%, there will be little genetic advance when there is little phenotypic variation.

The selection pressure is also important, because selection of only the few very best plants is likely to produce a greater advance than is selection of many moderately good plants, but at the expense of rapid loss in variation. Very strict selection will be most effective if the heritability is high. If the heritability is low (i.e., the environment has a large influence), many potentially good genotypes will not be selected if only a few plants are chosen. Thus it may be advisable to relax the selection pressure.

Discussion thus far has been general, directed to applied concepts that should prove useful to the breeder. The following discussion examines the effects of selection in somewhat greater detail. The aim is to gain an appreciation of selection effects on changing gene frequencies when dominance or recessiveness is involved, and with respect to initial gene frequencies. Consideration is also given to counteracting forces that tend to balance the effects of selection.

The strength of selection is expressed as a coefficient of selection "s." Generally, the contribution of the favorable genotype is taken as 1, and contribution of the less favorable genotype as 1-s. The value of s can vary between 0 and 1. For example, if s = 0.1, then for every 100 zygotes with the favorable genotype, there will be 90 of the less favorable one.

Consider the case of partial selection against the recessive genotype:

	AA	Aa	aa	Total
Initial proportion	p^2	$2pq$	q^2	1
Relative fitness	1	1	1-s	
After selection	p^2	$2pq$	$q^2(1-s)$	$1-sq^2$

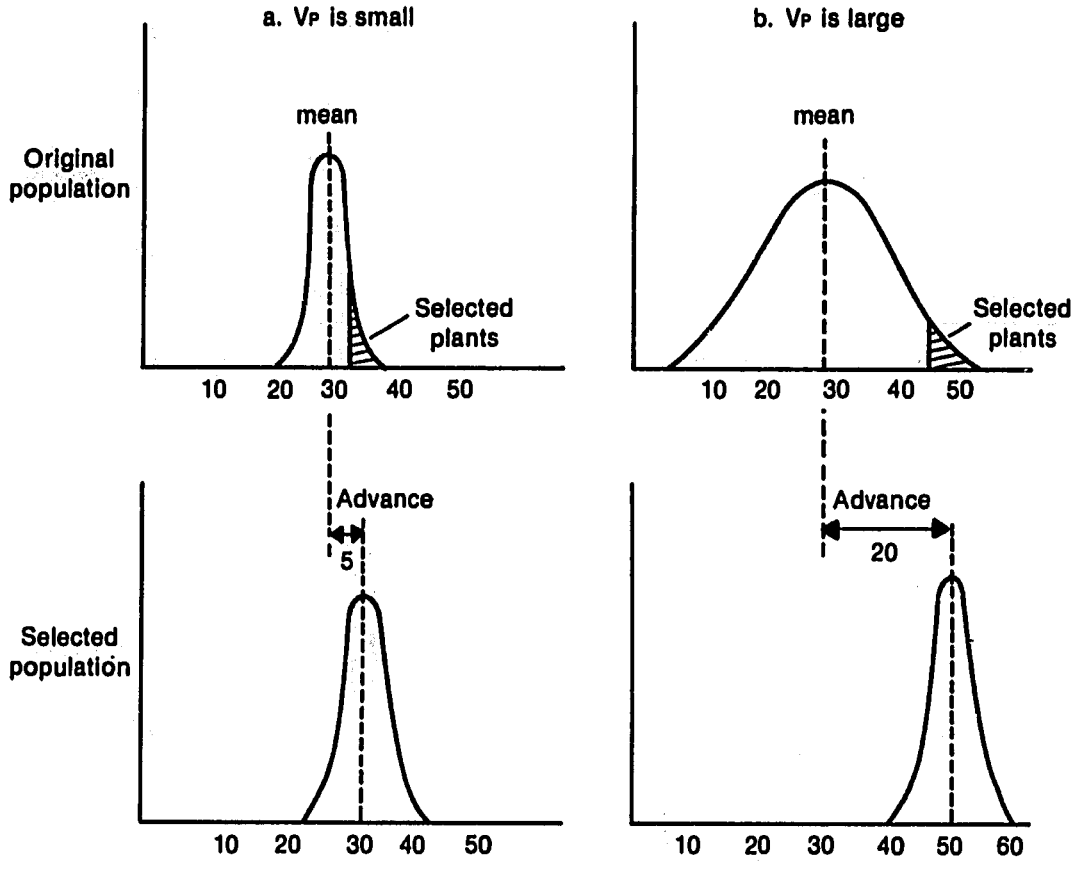


Figure 3.27: Genetic advance due to selection from populations with different values of V_P when H is large.

The total after selection is derived as follows:

$$p^2+2pq+q^2(1-s)$$
$$= (1-q)(1-q)+2(1-q)q+q^2-sq^2$$
$$= 1-2q+q^2+2q-2q^2+q^2-sq^2+1-sq^2$$

The frequency in the next generation can be determined as follows:

Remember that gene frequency can be found from the formula—

$$q = \frac{\frac{1}{2}H+Q}{N}, \quad \text{then } q = \frac{pq+q^2(1-s)}{1-sq^2}$$

Let p = 1-q and multiply (1-s) by q^2; the result is:

$$q_1 = \frac{q(1-q)+q^2-sq^2}{1-sq^2} = \frac{q-q^2+q^2-sq^2}{1-sq^2}$$

$$q_1 = \frac{q-sq^2}{1-sq^2} = \frac{q(1-sq)}{1-sq^2}$$

This equation can be generalized so that the relationship between any two generations becomes:

$$q(n+1) = \frac{q_n(1-sq_n)}{1-sq^2_n}$$

and the difference in gene frequency, Δq, between any two generations becomes:

$$\Delta q = q_1-q = \frac{q(1-sq)}{1-sq^2}-q$$

$$= q\frac{(1-sq)}{1-sq^2}-q\frac{(1-sq^2)}{1-sq^2}$$

$$= \frac{q-sq^2-q-sq^3}{1-sq^2}$$

$$\frac{-sq^2+sq^3}{1-sq^2} = \frac{-sq^2(1-q)}{1-sq^2}$$

The change in gene frequency for a number of different cases of dominance is presented in Table 3.1. These equations can also be represented graphically (Fig. 3.28).

The graphs and equations show that:

Selection is most effective at intermediate gene frequencies; it is least effective when the gene frequency "q" is either very large or very small. For example, when s = 0.2 and q= 0.99, Δq = -0.00244; when q = 0.5, Δq = -0.0263, and if q = 0.01 then Δq = 0.0000198 (Li 1958).

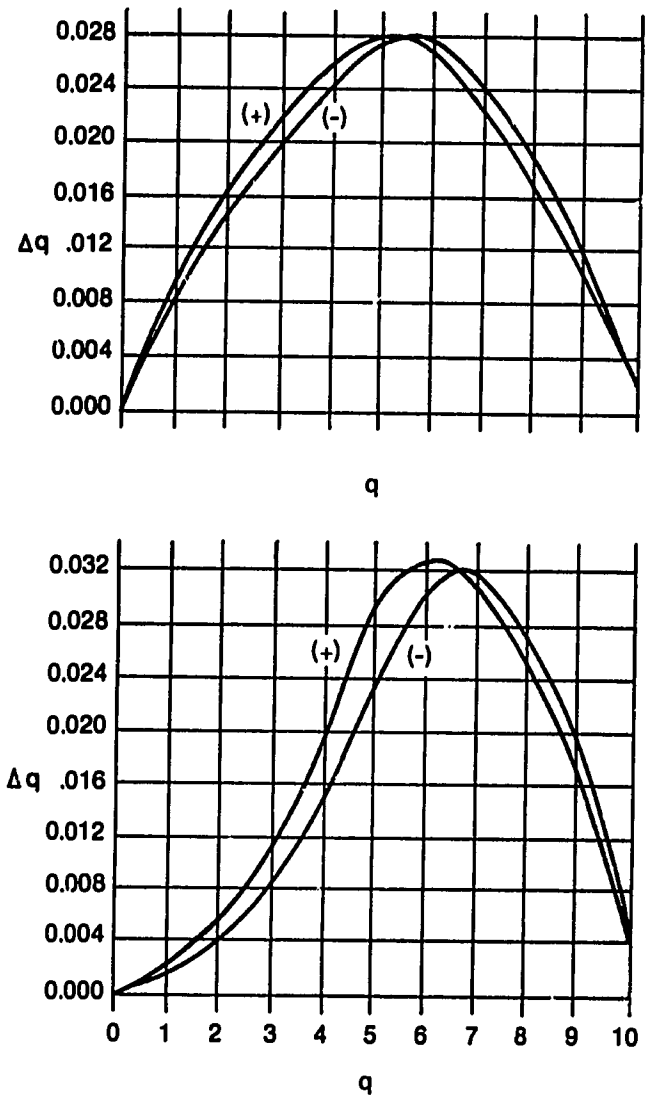


Figure 3.28: Changes of frequency, Δq, under selection intensity s = 0.2 at different values of initial gene frequency, q. Upper figure, an allele with no dominance; lower figure, an allele with complete dominance. The curves marked (-) refer to selection against the allele whose frequency is q, so that Δq is negative. The curves marked (+) refer to selection in favor of the allele, so that Δq is positive. (Source: Falconer 1964.)

Selection for or against a rare recessive allele is ineffective because a rare allele in a population is almost always found in the heterozygote.

The change in gene frequency from one extreme value of q to the other is shown in Figure 3.29. The negative sign (-) indicates selection against the allele, and the positive sign (+) indicates selection for the allele. A constant selection pressure of s = 0.2 is assumed.

It is apparent that the change in gene frequency begins slowly, increases at intermediate values of q, and then declines. Note also that the values of q tends toward the extremes of 1 or 0 (i.e., fixation or elimination).

When selection favors the heterozygote, the gene frequency tends toward an equilibrium at intermediate values of q—neither allele is lost. If s_1 = the selection pressure against the homozygote AA, and if s_2 = the selection pressure against the homozygote aa, it can be shown that the equilibrium values p and q are:

$$p = \frac{s_2}{s_1 + s_2} \text{ and } q = \frac{s_1}{s_1 + s_2}$$

These equilibrium values are dependent only on the selection pressure and are independent of gene frequency. No matter what the initial gene frequency may be, the equilibrium values of p and q will be same (Li 1958).

Consider the example where $s_1 = 0.15$ and $s_2 = 0.35$ against AA and aa respectively (Fig. 3.30).

Then at equilibrium

$$q = \frac{s_1}{s_1 + s_2} = \frac{0.15}{0.15 + 0.35} = 0.30$$

It has been found that in nature only a slight superiority of the heterozygotes in a population is sufficient to keep gene frequencies at intermediate values. It would appear that selection in favor of heterozygotes is common. Frequently genes are involved that have little effect (or that are nearly neutral) in the environment, so the selection pres-

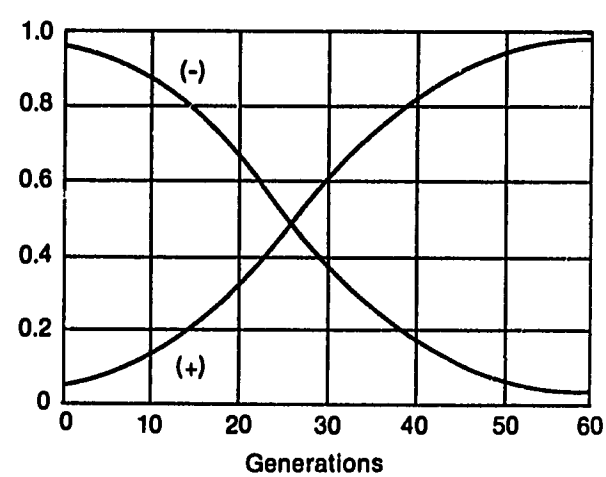


Figure 3.29: Change in gene frequency from one extreme value of q to the other with a constant selection pressure of s = 0.2.

Table 3.1: Change of gene frequency, Δq, after one generation of selection under different conditions of dominance.

Conditions of dominance and selection	Initial frequencies and fitness of the genotypes			Change in frequency Δq, of allele A_2	
	A_1A_1 p^2	A_1A_2 $2pq$	A_2A_2 q^2		
No dominance, selection against A_2	1	$1-\frac{1}{2}s$	$1-s$	$\frac{-\frac{1}{2}sq(1-q)}{1-sq}$	(1)
Complete dominance, selection against A_2A_2	1	1	$1-s$	$\frac{-sq^2(1-q)}{1-sq^2}$	(2)
Complete dominance, selection against A_1-	$1-s$	$1-s$	1	$\frac{-sq^2(1-q)}{1-s(1-q^2)}$	(3)
Overdominance, selection against A_1A_1 and A_2A_2	$1-s_1$	1	$1-s_2$	$\frac{+pq(s_1p-s_2q)}{1-s_1p^2-s_2p^2}$	(4)

sure is not strong. These are often found in the heterozygous condition, indicating the selective advantage for this situation. As a breeder moves uniform varieties from one environment to a different one he frequently observes the effect of residual heterozygosity.

Mutation

Mutations are generally recessive but can occur in the dominant condition. The mutation rate in both directions is constant and of the order of 10^{-4} to 10^{-6} (i.e., one mutation, A to a, in 10000 to 100000000 gametes). Mutations from the recessive to the wild type (normal) generally have been found to occur at about $^1/_{10}$th the rate of mutations from the wild type to the recessive. Mutation is the ultimate source of new alleles, thus the source of genetic variability. However, the effect of mutation on a population is so low that it is of evolutionary interest only and of little concern in an applied breeding program, i.e., mutation has a very low effect in changing gene frequency. (The use of mutation as a tool to obtain a desired trait is a different consideration, however.)

While mutation tends to increase genetic variability, most mutants are deleterious, and many are probably lost from a population. The probability that a mutation will be lost from a population after "n" generations is given in Table 3.2 (Li 1958).

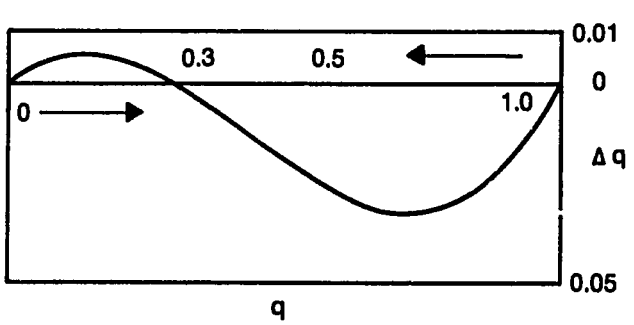


Figure 3.30: Approach to equilibrium with selection pressure against AA of s = 0.15 and against aa of s = 0.35.

Table 3.2: Probability of extinction of a single mutant allele.

Generation n	No. selective advantage Lost	No. selective advantage Retained	1% advantage Lost	1% advantage Retained
1	0.3679	0.6321	0.3642	0.6358
2	.5315	.4685	.5262	.4738
3	.6259	.3741	.6197	.3803
4	.6879	.3121	.6811	.3189
5	.7319	.2681	.7246	.2754
6	.7649	.2351	.7572	.2428
7	.7905	.2095	.7825	.2175
15	.8873	.1127	.8783	.1217
31	.9411	.0589	.9313	.0687
63	.9698	.0302	.9591	.0409
127	0.9847	.0153	.9729	.0271
Limit	1.0000	0.0000	0.9803	0.0197

This table shows that a mutant allele will be lost from a population if it has no selective advantage, and that the probability is greatest in earlier generations. If there is even a slight selection advantage, there is a probability that the allele will remain in the population indefinitely.

Mutation alters gene frequency because the mutational event occurs repeatedly at a constant frequency; therefore, even if some mutated alleles are lost, some will remain and become established in the population. In the absence of any other factors affecting gene frequency, an equilibrium value of p and q would depend only on the mutation rates. Let μ = the rate of mutation A to a and v = the mutation rate a to A; then the equilibrium values would be:

$$q = \frac{\mu}{\mu + v} \text{ and } p = \frac{v}{\mu + v}$$

These equilibrium values would be reached very slowly; in fact the mutation rates are such a small factor compared to other forces (such as selection) in changing gene frequency, that it is doubtful that these equilibrium values would ever be attained.

Joint Effects of Selection and Mutation

If mutation is in the same direction as selection, the rate of change in frequency will be increased. However, if they oppose (which is the usual case), a stable equilibrium would be reached that is independent of the gene frequency, depending only on the coefficients of selection and mutation:

$$q = \frac{\sqrt{\mu}}{s}$$

This equilibrium is stable, though it is approached very slowly—probably explaining why unfavorable recessives persist in natural populations instead of being lost. The existence of the recessive is maintained by mutation; hence Δq is generally very low. For example, if the mutation rate to the recessive mutant is μ = 0.000018, and the selection pressure against the recessive zygote is s = 0.02, the equilibrium population will contain μ/s = 0.0009 recessives, with $q = \sqrt{0.0009} = 0.03$. The recessive allele then exists mostly in the heterozygote: 2 (0.97) (0.03) = 0.0582, nearly 65 times as high as that of the homozygous recessive, i.e.,

$$\frac{2pq}{q^2} = \frac{0.0582}{0.0009} = 65$$

When q is very small, the recessive still exists in the heterozygote, and it is almost impossible to get it out of a population.

If the mutation rate (μ) is of the order of 10^{-5}, then only mild selection pressure is enough to keep the equilibrium at a very low frequency. For example,

- If s = 0.001, then $q = \sqrt{\mu/s} = 0.1$ and $q^2 = 0.01$
- If s = 0.01, then $q = \sqrt{\mu/s} = 0.03$ and $q^2 = 0.001$
- If s = 0.1, then $q = \sqrt{\mu/s} = 0.01$ and $q^2 = 0.0001$

Therefore, if an allele mutates at the rate of $\mu = 10^{-5}$, a selection of 10% (0.1) against the recessive zygote is enough to hold its frequency at 1 in 10000 (0.0001).

The discussion here deals with conditions of very low gene frequency, where changes by mutation and selection are very slow. Such effects are of evolutionary interest and of little practical concern to the plant breeder.

Subdivision and Migration

Natural populations are seldom found as random-breeding single units. Rather they are divided into subunits isolated by geographic, genetic, and physiological barriers. The division of large populations into subunits, known as *isolation*, can be partial or complete.

If a population is subdivided and random mating occurs within the subdivisions, then the effect is to reduce the frequency of heterozygotes and increase the frequency of homozygotes. Note the following in Table 3.3.

The population of heterozygotes in the total population, as well as in the subdivided populations, is less than would be expected if the total population were random mating. It also can be demonstrated that the variance in a subdivided population would

Table 3.3: Subdivision of a large population into five (K=5) random-mating groups of equal size.

Group	p_i	q_i	p_i^2	$2 p_i q_i$	q_i^2
1	.9	.1	.81	.18	.01
2	.8	.2	.64	.32	.04
3	.7	.3	.49	.42	.09
4	.5	.5	.25	.50	.25
5	.1	.9	.01	.18	.81
Total population	.6	.4	.44	.32	.24
Population if no subdivision			.36	.48	.16
Difference			+.08	-.16	+.08

be less than is the case if the total population were mating at random.

When populations are subdivided, there is an opportunity for migration between them. The effect of migration is to make the gene frequencies in the various groups more alike (more homogeneous). Migration is a counter force to subdivision in changing gene frequencies. (Note that the frequency of heterozygotes would increase.)

Migration also brings variation into a population. A breeder is using the effects of migration when he expands variation in his breeding program by introduction.

If migration is on a large enough scale, it can override selection pressure as a force in changing gene frequency. Sorghums cultivated along the Nile Valley in Egypt are predominantly durra, and genetic variation is small. It is reasonable to expect that the force of selection is relatively small, because the variability is small. It is probable that a massive introduction of germplasm and its interaction with the Egyptian durras would cause a change in the frequency of many genes—a greater change than could be caused by selection. Variation would increase and selection could be more effective.

In small subgroups of a random-mating population, there is a certain amount of inbreeding, represented as a coefficient of inbreeding F. The loss of heterozygosis is at a rate approximately ½ N per generation, where N is the number of individuals in the population. The effect of migration is to reduce this loss of heterozygotes; in other words, to counteract the effects of inbreeding.

Small Populations and Effective Population Size

Previous discussion has centered on large populations, with an analysis of how stable equilibrium values of the gene frequency might be reached. As the population size decreases, there is a random drift of the gene frequency (a *dispersive process*) that can be predicted in amount (probabilities), but not in direction. The effect of random drift can be greater than that of selection, migration, and mutation. If the population size is small, the gene frequency may vary greatly in the next generation. The change can be in any direction and is at random (note Table 3.4).

In such a population, if all loci had a gene frequency of 0.5, then they would vary in the next generation: more than 2% would have a frequency of 0.60 to 0.65. On the other hand, if there were one locus but many populations of 50 individuals, then in the next generation there would be small populations with different frequencies—2% of them with the frequency between 0.60 and 0.65.

Table 3.4: Probability distribution of q in a population of N=50 offspring from a parental population with q=0.5.

	q							
	.35	.35-.40	.40-.45	.45-.50	.50-.55	.55-.60	.60-.65	.65+
Probability	.002	.021	.136	.341	.341	.136	.021	.002

Source: Li 1958.

The random drift per generation in the color gene "non-Agouti" in three lines of mice, each maintained by six pairs of parents per generation, is shown in Figure 3.31.

The gene frequency in the three lines varied up and down at random, ranging from about 0.75 to 0.35 in generation 6 to 0.08 to 0.5 in generation 14. Eventually, the frequency will become 0 or 1, and all members of the small population will be homozygous for the gene, with frequency 1. If the frequency is "0," the gene is lost from the population. Eventually all genes will reach fixation (i.e., will have a frequency of 0 or 1).

The example above was of three lines of mice, each line with 12 individuals (six pairs). The practical consequences of small populations is of importance to the breeder trying to maintain a collection. If, for example, a breeder is seeking to maintain a collection by selfing five heads, it is obvious that there can be a great change in gene frequency, considerably changing the original collection.

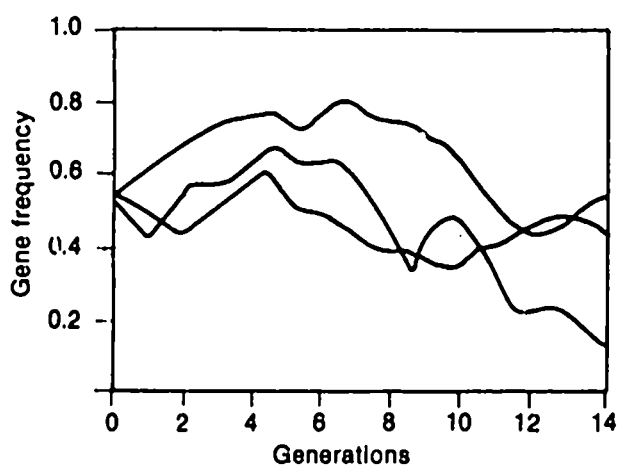


Figure 3.31: Random drift in the color gene "non-Agouti" in small populations of mice.

There is evidence to support the idea that random drift will cause considerable differentiation in a population size of 20; there would be moderate differentiation in a population size of 200; and for larger populations the amount of random drift would be negligible.

Summary

The concept of gene frequency has been described and illustrated. The breeder is interested in changing gene frequency, in enhancing the frequency of desired traits, and in maintaining or increasing variation in which selection can be effective. The factors of selection, migration (introduction), and population size are basic concepts that the breeder uses frequently. Mutation is of periodic interest to the breeder, but it is usually considered as a source of a desired trait and not as a factor in changing gene frequency.

Gene frequencies usually change most rapidly at intermediate values, and selection is very ineffective for recessive traits at very low or very high frequencies (approaching 0 or 1). Rare recessive alleles are usually found in heterozygous individuals. Both in nature and in breeding populations, there appears to be a selective advantage for the heterozygote, and alleles that have low selection pressure may remain in the heterozygous condition for many generations. Although genetic fixation does occur in nature, the stability and adaptation attained in individuals is impressive because mutation and selection, migration and selection, and subdivision and migration frequently oppose each other and selection favors the heterozygote. Many of these factors tend to keep gene frequencies at intermediate values and enable a population to respond to environmental changes. A breeder frequently requires some variation in a variety, yet wishes to maintain sufficient similarity so that it is phenotypically recognizable. The selective advantage of heterozygotes is known, and the breeder often finds that the heterozygote (hybrid) performs better than a relatively homozygous variety, particularly in harsh climates.

Population size is always a question in maintaining collections. If numerous sorghum collections are maintained side by side and allowed to open-pollinate, the effects of migration soon become apparent (first in the more open-headed types that outcross at a higher rate than the compact types). In avoiding the effects of small population size, the availability of land and cost of operations must be considered. There is usually a compromise between facilities and cost on the one hand and a desirable population size on the other. Collections should be maintained in their area of origin. When they are moved to a drastically different location, variation can increase tremendously, natural selection may eliminate some plants because they are not maintainable, and effective population size becomes a more critical consideration.

Obviously, those interested in plant breeding should have some clear working concepts of quantitative genetics and factors that influence gene frequencies.

Genetics of Sorghum

The Genetics of Maturity

Roy Quinby (1967), who has pioneered research on maturity and height in sorghum, identified factors at four loci that influence maturity, Ma_1, Ma_2, Ma_3, and Ma_4. Generally tropical types are dominant (Ma-) at all four of these loci, and a recessive condition (mama) at any one of them will result in more temperate zone adaptation (Table 3.5). In fact, the great bulk of lines used in the temperate zone have been found to be recessive at locus 1. Lines in a program to convert tropically adapted lines to temperate zone adaptation are likely recessive at locus 1 and dominant at the other three loci.

Genes at these loci interact: when dominance occurs at the Ma_1- locus, the dominant and recessive classes at the Ma_2, Ma_3, and Ma_4 loci can be identified in an F_2 population. When the recessive condition (ma_1ma_1) occurs, variation in time to flowering will diminish, making it difficult to separate genotypes (52.4 to 56.7 days' variation, compared to variation of 64.6 to 90.5 days when dominance occurs at locus 1—Table 3.6). If Ma_1 is dominant, Ma_2, Ma_3, and Ma_4 demonstrate dominance (lateness), but if the gene at locus 1 is recessive (ma_1ma_1), then the recessive ma_2ma_2, ma_3ma_3, and ma_4ma_4 may express dominance. There is an exception: when the gene at locus 1 is heterozygous (Ma_1ma_1) and that at locus 2 is recessive (ma_2ma_2), maturity is later than if both alleles at the Ma_2 locus are dominant (Ma_2Ma_2) (Quinby 1974).

Most of the lines from the tropical-to-temperate conversion program are recessive (ma_1) and dominant at the other loci. Yet the time to flowering varies from 60 to 85 days. Early-maturing tropical varieties tend to be early after conversion and late-maturing tropical lines tend to be late after conversion to

temperate zone adaptation. This is thought to be due to different alleles at one or more of the maturity loci, and not due to a group of modifying genes at other loci. The known alleles at the four maturity loci are listed in Table 3.7.

Effect of Photoperiod on Flowering

Sorghum is a short-day plant; i.e., the vegetative bud will remain vegetative until the daylength becomes short enough for the floral bud to develop. This point is called the *critical photoperiod*. Varieties have different critical photoperiods. Generally, tropical varieties will not flower in the temperate zones because the daylength during the summer period never becomes short enough to reach their critical photoperiod. By the time the daylength becomes short enough, the varieties are very tall and rank, the weather is cold, and the plants are usually killed by frost.

A description of the relationship between the short-day concept and photoperiod response can become quite complex. During summer months the daylength is longer in the temperate zone than in the tropics; the reverse is true in the winter, whereas the daylength tends to be the same (about 12 hr) at the spring and fall equinox. Varieties adapted to summer growth in the temperate zone generally have a higher critical photoperiod than those in the tropics; i.e., they will flower at longer daylengths than will tropical varieties. For example, a tropical variety may flower during days of less than 12 hours, when temperate zone varieties will also flower. As the plants are moved into the temperate zone, daylengths may exceed 13 hours. This is a longer day than in the tropics and exceeds the critical photoperiod of the tropical type—so it remains vegetative.

Table 3.5: Identification of sorghum varieties for dominance or recessiveness at four gene loci and their times of flowering at Plainview, Texas, USA, in 1964.

Variety	Genotype	Days to flower
100-day Milo (100M)	Ma_1 Ma_2 Ma_3 Ma_4*	90
90-day Milo (90M)	Ma_1 Ma_2 ma_3 Ma_4	82
80-day Milo (80M)	Ma_1 ma_2 Ma_3 Ma_4	68
60-day Milo (60M)	Ma_1 ma_2 ma_3 Ma_4	64
Sooner Milo (SM100)	ma_1 Ma_2 Ma_3 Ma_4	56
Sooner Milo (SM90)	ma_1 Ma_2 ma_3 Ma_4	56
Sooner Milo (SM80)	ma_1 ma_2 Ma_3 Ma_4	60
Sooner Milo (SM60)	ma_1 ma_2 ma_3 Ma_4	58
Ryer Milo (44M)	Ma_1 ma_2 ma_3^R Ma_4	48
38-day Milo (38M)	ma_1 ma_2 ma_3^R Ma_4	44
Hegari (H)	Ma_1 Ma_2 Ma_3 ma_4	70
Early Hegari (EH)	Ma_1 Ma_2 ma_3 ma_4	60
Combine Bonita	ma_1 Ma_2 Ma_3 Ma_4	62
Texas Blackhull Kafir	ma_1 Ma_2 Ma_3 Ma_4	68
Combine Kafir-60	ma_1 Ma_2 Ma_3 Ma_4	59
Redlan	ma_1 Ma_2 Ma_3 Ma_4	70
Pink Kafir CI432	ma_1 Ma_2 Ma_3 Ma_4	70
Red Kafir PI19492	ma_1 Ma_2 Ma_3 Ma_4	72
Pink Kafir PI19742	ma_1 Ma_2 Ma_3 Ma_4	72
Kalo	ma_1 ma_2 Ma_3 Ma_4	62
Early Kalo	ma_1 Ma_2 Ma_3 Ma_4	59
Combine 7078	ma_1 Ma_2 ma_3 Ma_4	58
TX414	ma_1 Ma_2 ma_3 Ma_4	60
Caprock	ma_1 Ma_2 Ma_3 Ma_4	70
Durra PI54484	ma_1 Ma_2 ma_3 Ma_4	62
Fargo	Ma_1 ma_2 Ma_3 Ma_4	70

Source: Quinby 1967

* Where the dominant symbol is used, the gene may be homozygous or heterozygous. Where the recessive symbol is used, both alleles are recessive.

Table 3.6: Floral characteristics of eight Milo maturity genotypes of sorghum grown from a 6 June 1969 planting at Plainview, Texas, USA.

Strain	Genotype	Days to floral initiation	Days to panicle development	Days to flower	Panicle weight
SM 100	ma_1 Ma_2 Ma_3 Ma_4	34	18	52.4+0.3	20.0+0.5
SM 90	ma_1 Ma_2 Ma_3 Ma_4	34	20	54.2+0.3	20.3+0.6
SM 60	ma_1 ma_2 ma_3 ma_4	34	21	55.3+0.2	23.2+0.7
SM 80	ma_1 ma_2 Ma_3 Ma_4	34	23	56.7+0.4	19.3+0.6
60 M	Ma_1 ma_2 ma_3 Ma_4	36	28	64.6+0.4	34.3+1.7
80 M	Ma_1 ma_2 Ma_3 Ma_4	40	29	69.0+0.2	30.8+0.9
90 M	Ma_1 Ma_2 ma_3 Ma_4	61	26	87.0+0.6	40.3+1.1
100 M	Ma_1 Ma_2 Ma_3 Ma_4	61	30	90.5+0.6	28.2+0.6

Table 3.7: Alleles at the maturity gene loci (Source: Quinby 1967).

Locus 1, Ma_1

- Ma_1^M - from Milo and in Fargo
- Ma_1^H - from Hegari and in Early Hegari
- ma_1^M - from Milo
- ma_1^F - from Bonita and Combine Bonita; came originally from Feterita or Blackhull Kafir
- ma_1^{B1} - from Texas Blackhull Kafir
- ma_1^C - from Combine Kafir-60 but of unknown origin
- ma_1^{B2} - from Redlan but originally from Blackhull Kafir CI 71
- ma_1^{P1} - from Pink Kafir CI 432, and in Kalo and Early Kalo
- ma_1^K - from Red Kafir PI 19492
- ma_1^{P2} - from Pink Kafir PI 19742
- ma_1^E - from Combine 7078 and probably in Tx 414 but of unknown origin
- ma_1^{B3} - from Caprock; originally from Dawn Kafir
- ma_1^D - from Durra PI 54484

Locus 2, Ma_2

- Ma_2^M - from Milo
- Ma_2^H - from Hegari
- Ma_2^F - from Bonita but originally from Feterita or Blackhull Kafir CI 71
- Ma_2^{B1} - from Texas Blackhull Kafir
- Ma_2^{B2} - from Redlan but originally from Blackhull Kafir CI 71
- Ma_2^C - from Combine Kafir 60
- Ma_2^K - from Red Kafir PI 19492
- Ma_2^{P2} - from Pink Kafir PI 19742
- Ma_2^{P1} - from Pink Kafir CI 432 and probably in Early Kalo
- Ma_2^E - from Combine 7078
- Ma_2^{B3} - from Caprock; originally from Dawn Kafir
- Ma_2^D - from Durra, PI 54484
- ma_2^M - from Milo and in Fargo and Kalo

Locus 3, Ma_3

- Ma_3^M - from Milo
- Ma_3^H - from Hegari and in Combine Bonita
- Ma_3^{B1} - from Texas Blackhull Kafir
- Ma_3^{B2} - from Redland but originally from Blackhull Kafir CI 71
- Ma_3^P - from Pink Kafir CI 432 and in Kalo and Early Kalo
- Ma_3^K - from Red Kafir PI 19492
- Ma_3^{P2} - from Pink Kafir PI 19742
- Ma_3^{B3} - from Caprock; originally from Dawn Kafir
- Ma_3^{B4} - from some Blackhull Kafir and in Fargo
- ma_3^M - from Sooner Milo
- ma_3^R - from Ryer Milo
- ma_3^H - from Early Hegari
- ma_3^F - from Bonita
- ma_3^D - from Durra PI 54484
- ma_3^C - from Combine Kafir 60
- ma_3^E - from Combine 7078

Locus 4, Ma_4

- Ma_4^M - from Milo and in Combine Hegari
- Ma_4^F - from Bonita but originally from Feterita or Blackhull Kafir
- Ma_4^C - from Combine Kafir 60
- Ma_4^{B1} - from Texas Blackhull Kafir
- Ma_4^{B2} - from Redlan but originally from Milo or Blackhull Kafir CI 71
- Ma_4^{P1} - from Pink Kafir CI 432
- Ma_4^K - from Red Kafir PI 19492
- Ma_4^{P2} - from Pink Kafir PI 19742
- Ma_4^E - from Combine 7078
- Ma_4^{B3} - from Caprock and from either Milo or Dawn Kafir
- Ma_4^D - from Durra PI 54484
- ma_4^H - from Hegari and in Early Hegari

The temperate zone type may have a critical photoperiod of 13.5 hours; thus a 13-hour daylength is still shorter than this critical period, and this variety will flower.

Figure 3.32 shows a group of lines drawn alongside a daylength axis, with each line representing the critical photoperiod of a variety. When the daylength is longer than the critical photoperiod, the variety will remain vegetative; when the daylength becomes shorter than the critical photoperiod (below the line), floral initiation will occur.

Daylength not only changes as one travels north or south from the equator, but changes with the time of the year. The change in daylength with time of year has essentially the same effect on floral initiation as does latitude (there may be some differences due to temperature). This effect can be shown graphically. Miller et al. made monthly sowings of varie-

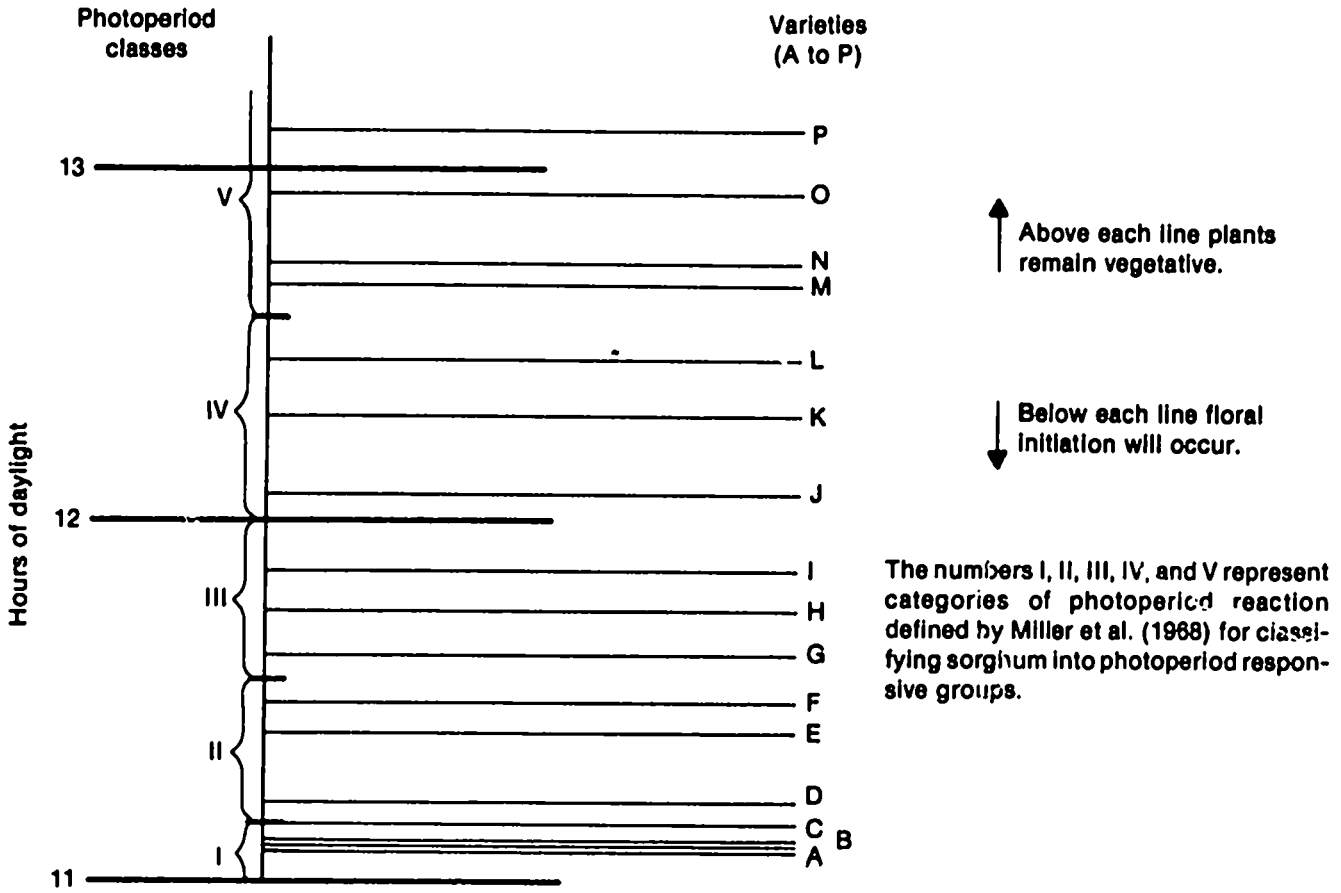


Figure 3.32: A scale indicating photoperiod reaction in relation to hours of daylight.

ties in each of these classes in Puerto Rico at 17.5° latitude and found the time from sowing to flowering to be as indicated in Figure 3.33 and Table 3.8. These data show that:

Class I: Flowering was delayed until sowings were made about September 12. Flowering occurred in early December, and days to flower were essentially the same for September, October, and November sowings.

Class II: Flowering was delayed more in sowings from February through May than in January. Sowings made in August produced slightly later flowering than those made in September and October.

Class IIIa: Flowering was delayed when sowings were made from March through August. The days to flower were low for sowings made in September and October.

Class IIIb: The flowering behavior was similar to IIIa, except that the time from sowing to flowering was more or less uniformly increased.

Class IIIc: The flowering pattern was somewhat like IIIa, except that the spread in days to flowering was less; particularly the days to flowering in March through May sowings were much less than in IIIa and IIIb.

Class IV: Flowering was delayed until the April sowing rather than March as for IIIa, b, and c; the spread in days to flower was somewhat less than for plants in IIIc.

Class V: The number of days to flower was more or less the same for sowings made in any month of the year. In other words, the critical photoperiod was never reached. If these sowings were made in a more northern latitude, Class V might need to be subdivided as was done for Class III;

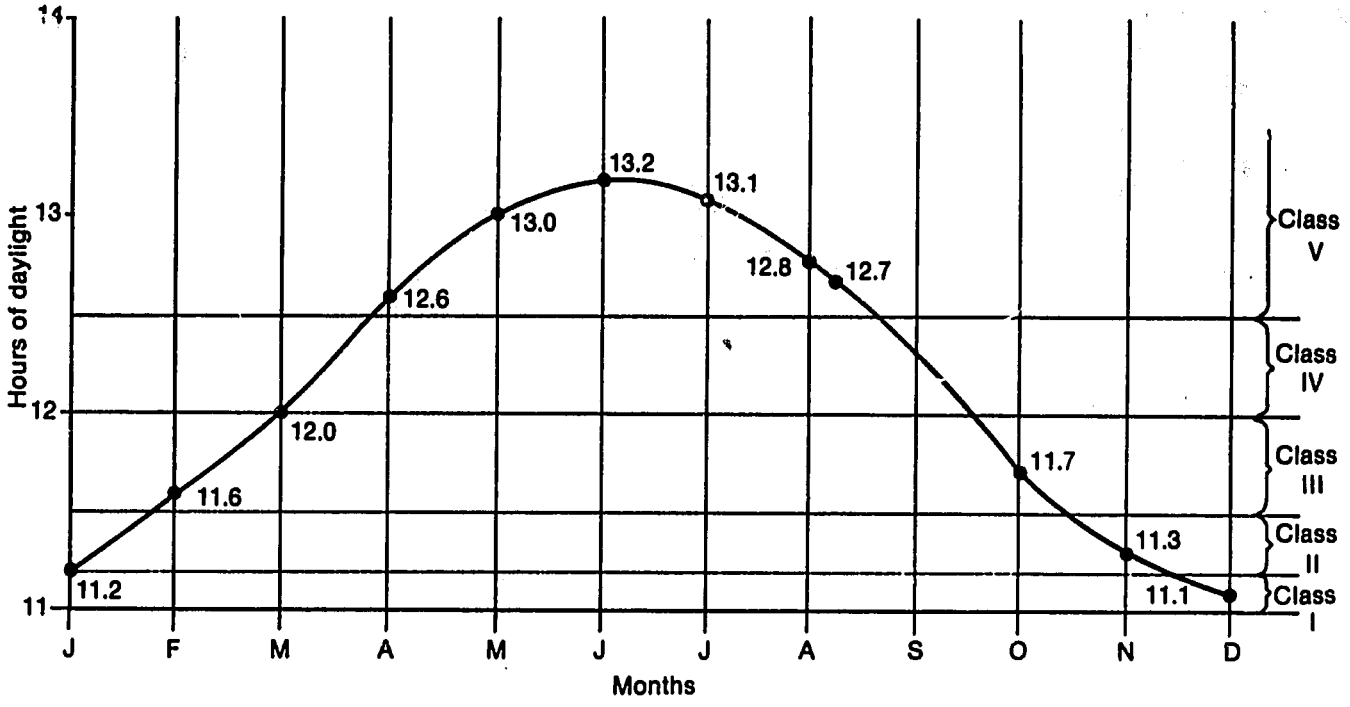


Figure 3.33: Curve of daylight hours for each month of the year at 17.5°N. Photoperiod classes are superimposed on this curve.

Table 3.8: Approximate days from sowing to flowering (anthesis), 17.5°N latitude.

Date of sowing*	Mean length of day (hr)	Class I	II	IIIa	IIIb	IIIc	IV	V
		——Days to flowering——						
January	11.2	310	155	75	110	85	70	75
February	11.6	270	280	55	110	75	70	60
March	12.0	250	240	220	225	100	75	65
April	12.6	210	200	195	195	105	110	63
May	13.0	185	170	155	180	105	112	70
June	13.2	155	140	125	150	90	100	60
July	13.1	120	125	95	115	80	80	60
August	12.8	100	105	75	95	75	70	63
September	12.2	82	100	55	75	60	65	58
October	11.7	80	100	50	70	50	60	58
November	11.3	82	105	60	80	60	60	60
December	11.1	120	130	100	110	85	75	70

*Sowings were made on approximately the 12th of each month.

i.e., some plants might reach a critical photoperiod and some not.

In the northern hemisphere, entries sown in a crossing block in September, October, or early November would require less stagger to achieve nick (see Glossary) between parents than would sowings at any other time of the year. By and large, sowings can be made successfully in January, but after early February (and particularly, after early March) some entries in a crossing block would be very much delayed in flowering and the crosses could not be made. Generally, lines with a critical photoperiod of about 12 hours or less cannot be used in the temperate zone. Nor can they be used in crossing blocks sown in some months of the year (March-April) in tropical locations without artificially reducing daylength to induce flowering. It is apparent that all lines flowering normally in a northern nursery would flower normally in a southern nursery; the reverse is not true—some lines might be very late or remain vegetative in a northern nursery.

Several of the Milo lines with known maturity genes were included in the monthly sowings made in Puerto Rico. The entries 100 M and 90 M were the only ones to show an effect of photoperiod (i.e., they were the only ones whose critical photoperiod was exceeded). These two entries are dominant at both the Ma_1 and Ma_2 loci. The genes Ma_3 and Ma_4 had no effect on photoperiod response at 17.5°N. They do have an effect in Texas (about 34°N), showing the effect of latitude (daylength) and the response of these plants to the larger critical photoperiods found at the more northern latitudes.

An appreciation of the photoperiodic response of sorghum is of great value to the breeder in planning crossing blocks and in assisting producers of hybrid seed.

The Genetics of Height

Genes at four loci in sorghum are important in the control of plant height. These genes are assigned the symbols Dw_1, Dw_2, Dw_3, and Dw_4. Tallness is partially dominant to dwarfness. The dwarfing effect of recessive genes (dwdw) at any of those four loci is brachytic in nature (i.e., the length of the internode is reduced, but not the peduncle length, head size, or leaf number, and the maturity is not changed). The zero dwarf type (dominant [DW-] at all loci) may reach a height of 4 m. The change from four to three dominant genes may result in a height change of 50 cm or more. If genes at one or more of the loci are recessive, the difference in height resulting from the recessive condition at an additional locus may have a smaller effect in reducing plant height. The difference between a 3-dwarf (recessive genes [dwdw] at three loci) and a 4-dwarf type may be only 10 or 15 cm.

There is variation in height between different varieties with the same genotype. This is thought to be due to an allelic series at a particular locus and not to modifying factors at other loci. There is instability at the Dw_3 locus; a dw_3 allele mutates to the dominant allele at a high rate (one mutation in 1209 gametes). Thus some sorghum fields may have a ragged appearance due to a greater frequency of tall plants. Some instability has also been found at the Dw_4 locus, but not at Dw_1 or Dw_2.

Table 3.9 shows the height and genotype of a number of sorghum varieties.

Tall hybrids can be produced from shorter parents using complementary factors. For example, a

Table 3.9: Height and days to bloom of certain sorghum varieties (1949 data from Chillicothe, Texas).

Serial no.	Cultivar	Genotype	Days to bloom	Ht to flag leaf (cm)
	Recessive for one gene:			
PI 54484	Durra	Dw_1 Dw_2 Dw_3 dw_4	62	159
PI 35038	Summac	Dw_1 Dw_2 Dw_3 dw_4	75	166
Agros 2650	Shallu	Dw_1 Dw_2 Dw_3 dw_4	91	157
FC 6601	Spur Feterita	Dw_1 Dw_2 Dw_3 dw_4	73	120
SA 1170	Tall White Sooner Milo	Dw_1 Dw_2 Dw_3 dw_4	62	127
SA 1295-89-2	Standard Yellow Milo	Dw_1 Dw_2 Dw_3 dw_4	89	173
CI 556	Standard Broomcorn	Dw_1 Dw_2 dw_3 Dw_4	74	207
	Recessive for two genes:			
FC 8962	Texas Blackhull Kafir	Dw_1 Dw_2 dw_3 dw_4	74	100
SA 79	Bonita	Dw_1 dw_2 Dw_3 dw_4	72	82
SA 281	Early Hegari	Dw_1 dw_2 Dw_3 dw_4	87	105
PI 34911	Hegari	Dw_1 dw_2 Dw_3 dw_4	96	126
SA 5155-31-29	Dwarf White Sooner Milo	dw_1 Dw_2 Dw_3 dw_4	61	94
SA 367	Dwarf Yellow Milo	dw_1 Dw_2 Dw_3 dw_4	83	106
CI 243	Acme Broomcorn	Dw_1 dw_2 dw_3 Dw_4	73	112
PI 30204	Japanese Dwarf Broomcorn	dw_1 Dw_2 dw_3 Dw_4	75	92
	Recessive for three genes:			
SA 5330	Martin	dw_1 Dw_2 dw_3 dw_4	63	61
SA 7005	Plainsman	dw_1 Dw_2 dw_3 dw_4	64	52
SA 1713-1	Double Dwarf White Sooner Milo	dw_1 dw_2 Dw_3 dw_4	66	53
SA 292	Double Dwarf Yellow Milo	dw_1 dw_2 Dw_3 dw_4	83	60

Source: Adapted from Quinby and Karper 1954.

2-dwarf hybrid ($dw_1Dw_2Dw_3dw_4$) can be produced from two 3-dwarf parents ($dw_1Dw_2dw_3dw_4$ and $dw_1dw_2Dw_3dw_4$).

Other Genetic Characters of Interest

Most of the information in this section is adapted from Doggett (1970) and Wall and Ross (1970).

Male-Sterility—Genetic

Male-sterility is caused by single recessive genes. Of these, ms_3 is most widely used because its expression of male-sterility is good and it is stable over many environments. Male-sterility caused by the recessive condition for ms_7 has been useful; also male-sterility caused by the antherless gene (al) has been found useful. Genetic male-sterility is used primarily in composites to enhance the level of recombination.

Male-Sterility—Cytoplasmic

Cytoplasmic male-sterility in sorghum makes possible the commercial production of hybrid seed. Male-sterility results from an association of Milo cytoplasm with sterility genes found primarily among kafirs but also in some varieties of other races. The genetics involved is not completely clear, but two genes (msc_1 and msc_2, when recessive in the presence of Milo cytoplasm) result in male-sterility. There are other factors that influence the sterility reaction, possibly having a modifying effect on the level of partial fertility. A technique for breeding against modifying factors is mentioned in the section on making new male-sterile seed parents (p. 115).

Disease Resistance

Kernel smut (*Sphacelotheca sorghi*)—three races of this disease are known, and resistance to each is controlled by an incomplete dominant, Ss_1, Ss_2, Ss_3.

Head smut (*Sphacelotheca reiliana*)—in most varieties resistance is dominant to susceptibility.

Milo disease (*Periconia circinata*)—reaction to this disease is controlled by a single locus (Pc). Susceptibility is partially dominant; the F_1 is intermediate.

Anthracnose (*Colletotrichum graminicola*)—susceptibility on the leaf is controlled by a simple recessive gene (l). Susceptibility to the stalk rot phase of this organism is controlled by the simple recessive (ls).

Rust (*Puccinia purpurea*)—susceptibility is controlled by a simple recessive gene (pu).

Leaf blight (*Exserohilum turcicum*)—most grain sorghums are resistant. Susceptibility in sudangrass is inherited as a simple dominant.

Charcoal rot (*Macrophomina phaseolina*)—inheritance of resistance is recognized but has not been analyzed completely; apparently more than one gene is involved.

Downy mildew (*Peronosclerospora sorghi*)—resistance is inherited as a recessive character. A number of types, including most of the kafirs, are resistant. Sudangrass is susceptible.

Maize dwarf mosaic virus—resistance is dominant; the genetics are not known.

Insect Resistance

The genetics of insect resistance are not well understood. Generally it appears to be multigenetic, and complete resistance is seldom found.

Midge (*Contarinia sorghicola*)—recently entries have been identified in the Texas Station USDA Conversion Program that show a high level of midge resistance.

Shoot fly (*Atherigona soccata*)—resistance is found at a low but useful level. There are apparently three aspects: (1) nonpreference for oviposition; (2) antibiosis (i.e., plant resistance per se); and (3) recovery resistance (tillers form after the main stem is destroyed and survive to make a crop). Recently the presence of trichomes (microscopic hairs on the lower surface of leaves) has been found to contribute to oviposition nonpreference. The presence of trichomes is controlled by a single recessive gene.

Stem borer (*Chilo partellus*)—variation in resistance is generally found at a relatively low level.

Storage insects—small corneous grains store better than large soft ones.

Stalk Dryness and Sweetness

Dry stalks are controlled by a simple dominant gene, D; juiciness is recessive. Dry stalks have a

white leaf midrib; juicy stalks have a dull green leaf midrib (possibly with a narrow white strip in the middle). An insipid stalk is controlled by a single dominant gene, X; sweetness being recessive. There is apparently no linkage between the genes at loci controlling the dry-juicy and insipid-sweet characters. There is no clear evidence favoring either sweet or nonsweet stalks for forage; livestock eat both.

HCN Content

Sorghum produces HCN, which may be dangerous when the crop is used for feed. The problem is particularly acute in seedlings or on regrowth of a ratoon crop and is aggravated by drought and low temperatures. Inheritance seems to be controlled by more than one factor, and in many cases low HCN content shows partial dominance.

Plant Colors

Genes for plant color influence the green portions of the plant—leaves, stems, glumes. The gene P- produces a purple color, and recessive plants (pp) are tan. The shade of purple pigmentation is influenced by alleles at the Q locus; purplish-black is due to the allele q and reddish-purple is due either to the Q or q^r alleles.

Glume colors are controlled by the same two loci (P and Q). Black and red glumes are dominant (P-), and mahogany or sienna glumes are recessive (pp). There appear to be inhibitors causing the glume colors in some plants to fade.

A red pigment appears in dead leaves and sheaths in red-seeded varieties, but not in white-seeded ones. Genes R-yy are responsible for red pericarp color and for this effect in dead leaves. The Q gene influences color in plant sap (spots on white-seeded varieties are red in red-pigmented plants and purple black in purple-pigmented plants.)

Grain color is determined by pigmentation of the pericarp, testa, and endosperm. Color in these tissues is controlled by different sets of genes. Genes for grain color are:

- Ce: Plant color is present in the testa and the glume cup (Q is expressed).
- B_1, B_2: Cause a brown testa (when both genes are found in presence of ce); B_1b_2, b_1B_2, B_1B_2, and Ce B_1B_2 have colorless testas.
- S_1: Testa spreader, in the presence of B_1 and B_2, results in brown color in the epicarp (outer layer of the pericarp).
- Y: Epicarp yellow color (in rrY- condition) versus white (yy condition).
- R: Epicarp is red if Y is found; otherwise it is yellow or white.
- I: Intensifies color of the pericarp (epicarp); Bw_1 and Bw_2 are complementary factors; when both are found, there is a brown wash on the seed.
- M: Causes a colored wash on the seed.
- Pb: Causes purple blotching of the seed.
- Pt: Causes a purple tip on the grain.

Martin (1959) has indicated the genotype of several different colored grains, as shown in Table 3.10.

Endosperm Characters

Wx (waxy) results in a starch with a normal amylose-amylopectin balance; when homozygous, the

Table 3.10: Genotype of sorghum seed colors.

Type variety	Seed color	Epicarp	Testa	Testa spreader
Blackhull Kafir	White	RR yy II	b_1 b_1 B_2 B_2	SS
White Milo	White	RR yy ii	b_1 b_1 B_2 B_2	SS
Club Kafir	White	RR yy II	b_1 b_1 B_2 B_2	ss
Shallu	White	RR yy ii	B_1 B_1 b_2 B_2	SS
Feterita	Bluish white	RR yy ii	B_1 B_1 B_2 B_2	ss
Yellow Milo	Salmon pink	RR YY ii	b_1 b_1 B_2 B_2	SS
Bonar Durra	Lemon yellow	rr YY ii	b_1 b_1 B_2 B_2	SS
Red Kafir	Red	RR YY II	b_1 b_1 B_2 B_2	SS
Sourless Sorgo	Buff	RR yy ii	B_1 B_1 B_2 B_2	SS
Schrock	Brown	RR yy ii	B_1 B_1 B_2 B_2	SS
Darso	Reddish brown	RR YY II	B_1 B_1 B_2 B_2	SS

Source: Martin 1959.

recessive allele wx results in a waxy endosperm, i.e., a predominance of amylopectin.

Su (sugary) gives normal sugar content, while the recessive (su) condition results in a high sugar content. Seeds are usually dimpled and the stems are usually sweet.

Z causes greater endosperm hardness than the homozygous recessive z, which produces a chalky condition.

Yellow pigment in the endosperm is not well understood, but it appears that more than one major gene or modifier is involved. The yellow color is due to xanthophyll and carotene pigments.

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SECTION 4
SORGHUM IMPROVEMENT

METHODS AND PROCEDURES

Section 4 deals with the practical aspects of plant breeding. As described in the previous section, breeding is controlled evolution whereby plants are changed rapidly in a direction of interest to the scientist. A breeding principle is that improvement by selection depends on the availability of variation. Quick gains are possible through breeding, but usually there is a rapid loss in variation, with yield increases approaching a plateau. Thus the breeder must be concerned not only with gain in the traits of interest; he also must strive for maintenance of variation. Introduction (migration) from collections and other breeding programs and the use of mutagenic agents are important in expanding variation. Variation can also be expanded by various forms of crossing.

General concepts covered in Section 4 include:

- The functions of collection and introduction; processes basic to maintenance and expansion of variation available to the breeder.
- Pedigree nomenclature in relationship to pedigree breeding and crossing. Several systems are described, ranging from a "one-station, one-season" breeding situation to those with many stations and more than one season per year. Such systems are useful if a nation wishes to develop a coordinated improvement program.
- Commercial use of F_1 hybrids involving use of cytoplasmic male-sterility.
- The naming of varieties and hybrids.
- Expansion of variation by crossing and/or backcrossing, followed by selection. Frequently crosses between adapted introductions and local types are valuable as source material from which to select new lines or parents for hybrids. Crossing procedures are described.
- Development of composites and breeding procedures. These allow the breeder to use some techniques of primarily cross-pollinated crops.
- Breeding for resistance to disease and insect pests.
- Breeding for food quality.

Some Basic Working Concepts

A major aim of this book is to provide a broad view of sorghum improvement for young scientists and field technicians—particularly breeders. These readers are asked to see the major objective as crop improvement and not simply the development of a new variety or hybrid. The breeder should be a part of a multidisciplinary team. Insect or disease problems, economic policy, and social implications, for example, often spell the difference between success or failure of a program.

The traditional varieties of sorghum have been accepted for various uses that have value to the users. The idea of a varietal change frequently meets opposition even from scientists, because of a

feeling that change will not be accepted. To make progress, this attitude must be changed—if the farmer gains from a new variety or practice a change will likely take place. The scientist must be willing to explore new avenues so that he does not "lock" the farmer into the old tradition.

Some attempts have been made to improve varieties or hybrids by introduction, in order to avoid plant breeding in local programs to increase production. The chance of success is low, because good adaptation usually requires local selection. Frequently, more time is spent on introduction and evaluation than would be required if plant breeding was initiated in the beginning.

As new programs begin against a traditional background where local landraces of a fairly narrow genetic base are in use, identification of agronomic superiority is frequently neither difficult nor time consuming (3 to 5 years). This is the beginning of the job—as new varieties and hybrids (involving introduced parentage, coupled with a change in management) move to the farmer, there is often an increase in insect and disease problems. In order to respond to these changes the program emphasis may well shift after 6 to 12 years so that the major effort is breeding for resistance to insects, disease, drought, *Striga*, and the improvement of grain quality. Solution of these problems requires a research organization, which should be implemented at the beginning of a crop improvement project—particularly when shifting away from long-established traditional agriculture.

The variation found within the sorghums traditionally used is small in many locations, i.e., the germplasm base is narrow. Selections from collections made within a region or from crosses between them usually result in little gain in yield. Further advance by manipulating local, phenotypically similar plants is likely to have limited reward.

Frequently, traditionally used varieties are tall, sometimes late, will not stand high population levels, and lodge. Their response to improved management in terms of increased grain yield may be disappointing and lodging may increase. Some varieties are more responsive to management practice than others—and a breeder wants to work with responsive types.

An important requisite of sorghum improvement is to have available an array of varietal types, so that the scientist has a better selection opportunity. Genetic variation in sorghum breeding programs can be expanded in several ways: (1) use of the world collection; (2) requesting seeds from other breeding programs; and (3) by breeding procedures, such as the formation of composites, which retain a high level of variability.

A breeder is generally successful in direct proportion to his familiarity with the plants that he breeds. As a program begins, or where there is diverse germplasm, it is more important to look at many entries with a minimum of notes, than to attempt to describe a small number of entries in detail.

The fastest progress toward the development of superior lines may be possible by pedigree selection within new introductions (accessions). As a beginning, a large array of diverse lines should be collected from many different locations in the world. Initially, selection can be done visually and then, after a few generations, by yield trial evaluation, which rapidly reduces the number of different entries and the genetic variance on which selection is based.

Breeders' stocks acquired from other programs usually are more immediately useful (from a general agronomic point of view) than are accessions of unselected varieties. A free exchange should exist between breeders the world over. (Breeding achievements are based on use, not acquisition and possession.)

Genetic variation can be sustained if crosses are made between selected lines. Segregation will occur in the F_2 and advanced generations, and pedigree selection for the development of superior lines is effective in the segregating generations. Genetic variation can also be sustained in composites. Genetic sterility is frequently introduced into such composites to increase the level of outcrossing and to make it easier to use some of the breeding procedures for populations. Selection of lines entered into composites is based on criteria such as yield, disease resistance, drought tolerance, etc. After entries have been selected, they are crossed and backcrossed to a source of genetic sterility.

Pedigree selection in introductions or local lines is useful in developing elite varieties quickly; selection from advanced generations from crosses serves as a source of new entries for the breeding nursery. Composites require time to develop, but are useful as a continuous source of new breeding material. The composite should be improved over time, and should then be a source of higher-yielding lines. Obviously, each of these processes is important to a breeding program, and all should be in process simultaneously.

Experience has indicated that sorghum varieties that perform well under high levels of fertility also will show comparatively better performance under poor levels. There is a greater interaction of varieties

with moisture deficiency, requiring evaluation in these conditions. The differences in yield response between varieties are greater at high yield levels (6 to 8 t/ha) than at low levels; hence it is easier to select at the higher levels. A useful differential in plant response may even disappear at very low levels of yields. It is recommended that nurseries be grown at high levels of fertility, with good management to maximize the selection opportunity. However, yield trials should be grown based on a recommended package of practices and with moisture conditions similar to those used by the farmer.

Insect control should be nominal in a nursery—the nursery should not be overprotected by uneconomic applications of insecticides, and it should not be left so unprotected that it could be destroyed. Selection should be made for insect resistance, if possible, and insecticides should not be used in such a way that the selection opportunity is lost.

Good levels of moisture and fertility permit the selection of high-yielding responsive varieties, while a moderate level of plant protection permits selection for resistance to the insect pests of the region. These comments about moisture, fertility, and plant protection may appear contradictory, but it should be noticed that they are all in the direction of maximizing differences between entries in the nursery.

Agriculture in many developing nations, especially those in the tropical zones, could be much more intensive. Short-duration varieties that fit into a crop-sequence scheme should be considered. The problems arising from the use of short-duration varieties are worth solving if cropping can become more intense—the crucial concept is yield per unit area per unit time, rather than yield per unit area only.

The most rapid progress can be made if the breeder is a member of a team that includes an entomologist, pathologist, physiologist, agronomist, etc. (Teamwork builds team spirit; there is plenty of credit for everyone if a real contribution is made.)

The World Collections of Sorghum and Millets

Background

Large collections of sorghums and millets have been established. In 1957 K.O. Rachie brought a collection of sorghums from Mexico to India when he participated in the Indian Agricultural Program of the Rockefeller Foundation. During 1959 to 1962 he organized the collection of sorghum and millets in India; he also received collections organized by other breeders (primarily in Africa and the USA). The accumulation of existing collections (Table 4.1) was further strengthened by requests made via the National Science Foundation of the USA. These collections continue to increase; currently they are actively maintained in the USA (Purdue University and the United States Department of Agriculture) and by ICRISAT. The collections are in long-term storage at the seed repository at Fort Collins, Colorado, and at ICRISAT Center.

The collections were initially established in support of the crop-improvement programs in India, then expanded to world collections. The sorghum and pearl millet collections have been most used and have been screened in several parts of the world. A number of measures of morphological characters have been made in the sorghum collection; these have been printed as a special publication of the Indian Society of Genetics and Plant Breeding (Murty et al. 1967). A sizeable portion of the collection has been evaluated for tolerance to the shoot fly, *Atherigona soccata*, and the stem borer, *Chilo partellus* (Anon.).

There are other listings of sorghum entries showing resistance to a number of diseases: Rust (*Puccinia purpurea*), downy mildew (*Peronosclerospora sorghi*), sugary disease (*Sphacelia sorghi*), leaf blight (*Exserohilum turcicum*), grey leaf spot (*Cercospora sorghi*).

Table 4.1: Relative sizes of existing collections of sorghum and millets.

Scientific name	Common name	Approximate number of accessions
Sorghum bicolor	Sorghum	16 587
Pennisetum americanum	Pearl millet	12 431
Eleusine coracana	Finger millet	662
Setaria italica	Foxtail millet	733
Panicum miliare	Common millet	214
Panicum miliaceum	Proso	155
Paspalum scrobiculatum	Kodo	254
Echinocloa colonum	Barnyard millet	345

Information about the sorghum collection continues to be accumulated at other locations. Futrell and Webster (1966b) have collected and published data indicating resistance to downy mildew in a substantial portion of the world collection. They did the same (1966a) on races of sorghums resistant to sooty stripe (*Ramulispora sorghi*). John Axtell and R.C. Pickett at Purdue University (Indiana, USA) have screened the world collections for protein content, lysine, and other amino acids.

Data will continue to accumulate as more scientists in different parts of the world make use of the collection. The relevant results of most of this research will appear in published form; some will appear in project reports, etc. The publications and reports will normally be read by others interested in the same general problems. Thus existing publications and reports are used to spread information about the collection. It is important, as part of the collection function, that such published information be accumulated for use as reference material. Relevant descriptors of the sorghum and pearl millet collections are being accumulated in several places in the world in standard format, and the data are being processed by computer. Descriptors for sorghum are described in Appendix 2. The computer can be used to help identify entries with a particular set of traits; catalogs can also be printed.

The sorghum collection has provided a broad germplasm base for building the breeding program in India. Only one section of the collection, the yellow endosperm types, has been used extensively. These types (when crossed with Combine Kafir 60—a cytoplasmic male-sterile seed parent) resulted in a hybrid that yielded well, had a grain quality similar to the local preference, and threshed easily. Recently, other entries in the collection have been used more extensively, but primairly as parents in crosses from which new lines have been selected. The whole collection has been useful as a source of insect and disease resistance and in screening for protein quality. The collection has been vigorously screened for tolerance to shoot fly. Several forms of resistance have been identified: antibiosis, recovery resistance (tillers survive after main culm is killed), and oviposition nonpreference. These forms of resistance have been used with varying degrees of success.

Remaining Considerations for Study

Some entries have been difficult to maintain at Hyderabad, India, and it has been difficult to build up a large supply of seed; thus the need for frequent multiplication. It is known, for example, that the vigor of entries from the Ethiopian Highlands is very much reduced when they are grown in Hyderabad. Such problems support the concept that collections should be increased in (or close to) the area of origination, so that the collections are maintained in adequate quantity and in their original form.

Adequate description of the agronomic characteristics of a collection is difficult. Scientists have been invited from throughout India to make their own selections from the sorghum collection as it was being increased or screened. Scientists in the USA have been able to see the collection in Puerto Rico. The sorghum and pearl millets collections are now being described using standardized descriptors. Entries of interest can be identified by computer processing of the descriptor information. Good records about the origin of collections is lacking, and in many instances the information is not available at the place where the collection was made. Collections of wild and weedy relatives are virtually absent. This suggests the need for pretraining of collectors.

Maintenance and distribution of collections is expensive. Many crop improvement projects are pressed for adequate funds and facilities, and it is difficult to add the functions of collection to a breeding program unless the program is specially funded and staffed.

To insure their safekeeping, collections should be kept in long-term storage in at least two places in different parts of the world so that if a collection at one location is damaged or destroyed at least one other remains for agricultural and scientific uses.

Sorghum is a tropical grass; it has been adapted to grow at latitudes as far as 45° from the equator. However, because of photoperiod problems, many collections adapted in the tropics will not flower at high latitudes. The United States Department of Agriculture (USDA) and the Texas Agricultural Experiment Station, as well as several commercial companies in the USA, have begun to convert these tropical types to shorter and less photoperiod-sensitive types. The conversion is primarily a backcrossing process, where the short-early type is the nonrecurrent parent. Crossing and backcrossing is done at a tropical location: the Federal Station, Mayaguez, Puerto Rico (17° N). The segregating generations are grown at a more northern location: the Chillicothe and Plains Research and Extension Station of the Texas Experiment Station, Lubbock, Texas (34° N). The short-early segregates are sent back to Mayaguez for the next cycle of backcross-

ing and selfing (the cycle requires 1 year). After three or four cycles of backcrossing the exotic type is recovered, but it is short and essentially photoinsensitive. Breeders in the USA have been keenly interested in this conversion program because of the tremendous array of new genotypes available for their use. Breeders in the tropics are interested in the entries from this program (either fully converted or partially converted) for use in selecting new lines.

The accession numbers assigned when these collections were initiated are now used internationally. Indian Sorghum (IS) numbers were assigned originally to sorghum accessions; Indian Pennisetum (IP) numbers were assigned to the pearl millet collections, etc. Within India, the IS number was retained as a pedigree by any station using the entry, and the location and season were added as an origin; this, in fact, made a complete pedigree. Thus IS 534 sown at Hyderabad in row 25 during the 1970 *kharif* season would have the pedigree: IS 534 Hyd 70 K 25. The same entry sown at Coimbatore in row 105 would have the pedigree: IS 534 CO 70 K 105. The USDA has agreed to use IS numbers rather than the PI numbers previously used by them for the sorghum collection. Entries from the conversion program retain the IS number, but a "C" is appended; i.e., IS 534 C. The IS numbers were retained as these collections were used in the Near East, with appropriate symbols to indicate location and season. These agreements reflect continued effort toward avoiding a proliferation of numbers associated with the same entry.

Types of Collections Recommended for Development

The Rockefeller Foundation organized several committees to study the problem of germplasm collection and preservation of several important crops. This activity is now the responsibility of the International Board for Plant Genetic Resources (IBPGR). J.R. Harlan served as chairman of The Rockefeller Foundation-sponsored committee concerned with sorghum and millets. The recommendations of the committee about the types of collections to be developed are as follows:

Accessions Collection: seed of every collection is saved. This reduces the chance for genetic loss by discarding apparent duplicates and the masking of useful traits by bulking.

Basic Collection: A two-way stratification based on (1) race, subrace, geographic distribution, and adaptation, and (2) traits of economic importance (insect and disease resistance, combining ability, nitrogen responsiveness, etc.). Careful evaluation is required, drawing on the experience of workers in various parts of the world to develop this collection.

Spontaneous Collection: Consists of wild and weedy races. This is to be maintained separately, primarily because of special management required and because some types are a nuisance as weeds.

Bulk Collections: A series of bulks to be established by compositing similar materials. Care should be taken that valuable traits, such as resistance to an insect pest, are not lost in the bulking process. Special bulks might be created of varieties with some special attribute. Entries in any one bulk should be similar in origin, height, maturity, and adaptation.

Named Variety Collection: Includes improved varieties (not hybrids) named and released by private and public institutions. At some time, these have been considered outstanding, and such elite germplasm might well have continuing value.

Genetic Stocks Collection: Includes stocks with known genetic factors, translocations, inversions, or other special traits—also lines with resistance to particular races of pathogens, insects, etc. This would be a gene bank.

Population Collection: Populations created from carefully selected entries to conserve germplasm and also to be improved by selection. This objective is to provide base material for breeding programs of the future.

The basic collection as well as the bulk and population collections should be stored at several locations, and could be kept in conjunction with a major crop-improvement program. As quarantine regulations gradually become more restrictive, it is increasingly difficult to move seeds freely. It would be useful if basic or working collections could be maintained on the continents where the crop is of interest. This would help solve the quarantine problem, and would reduce the burden on any one location for supply of seeds. It also would provide a location for the increase of the part of the collection adapted in that area.

The maintenance of a voucher sample of entries in the collection is important, particularly for the basic collection. Each time the collection is increased, there is a chance for error due to handling, and there could be changes due to problems such as sample size and environmental influences. Ideally, a herbarium of voucher samples should include the head at flowering time, the head at maturity, the flag leaf, and at least one other leaf, including the leaf sheath and two nodes. If such

elaborate voucher samples cannot be developed, it would be helpful to include the head at maturity. Frequently, a given sample is not uniform, and several heads may be required to represent the collection. The voucher samples can easily be taken from the first increase following collection.

Frequently, collections are made by scientists sent from one part of the world to another for this purpose. These collectors have limited time and can inspect only the maturing portion of the crop and its wild relatives. Market samples help expand this array. Although much useful material has been collected in this way, there is always uncertainty as to the adequacy of the collecting process.

Collections can also be done by resident collectors (i.e., people who live in a region) who can make periodic trips throughout the region over an appropriate period of time. Within a country, there may be several such persons working at regional experiment stations. These individuals can be trained so that they recognize the appropriate cultivated and wild types. They can properly record the location where a collection is made, as well as information about local use of the entry. Such collectors should be effectively supported so they can move at appropriate times and travel into remote areas, if necessary. They also should be well motivated and dedicated to the project.

Collections made in any region should be included in the world collection so that they may be moved into breeding programs around the world.

Pedigree and Cultivar Nomenclature

Pedigree Systems

A pedigree system should provide a name for each discrete type; it should show relationship (sister lines); and it should make it possible to identify the breeding history clearly, i.e., to trace back through the generations of development.

Characteristics of a pedigree system are:

- Brevity
- Simplicity
- Readability
- Understandability
- Completeness
- Built-in safeguards against errors

Many pedigree systems are used by plant breeders. The following discussion deals with the various considerations in establishing a pedigree system.

Basic Uses and Notations

When a breeder requests seeds from other breeders, he receives seed identified by the pedigree system of the supplier. Frequently a breeder will want to identify such new accessions in his breeding by his own pedigree system; however, if a line is widely known by a particular pedigree, it may be desirable to retain that pedigree. In any case, the pedigree used by the supplier is written into the accession register of the receiving breeder.

Accession books and field books are used continuously. The greatest use comes in organizing seed for nurseries and trials and in filling seed requests; it is convenient to be able to trace back through pedigree records to find seeds in the seed store. At times, it is desirable to re-request seeds of some varieties, either because the entry was lost or because a larger quantity is required. At times, it is necessary to go back into the records to correct pedigrees—copy errors occur. Some lines are eventually released to farmers and it is simple courtesy to acknowledge the station that provided the accession. Thus, it is necessary to trace back through the breeding history to the accession book to confirm the sender's name. Pedigree records and the accession book are useful in organizing planting plans, as well as in summarizing data and writing reports.

Several situations may arise that require a slightly different notation. The simplest case is that of a breeding program at one location that might be working independently of other locations. The system becomes a bit more complicated if it involves a second season, or second location (such as a tropical location for winter breeding), so that more than one generation per year is possible. A third possibility might involve breeders at several locations in a country working closely in a cooperative program—pedigree notation might have certain common characteristics, but station identification would be desirable.

Notations include those used:

- on seed samples received,
- during early-generation breeding,
- on "fixed" lines,
- on released lines,
- for hybrids in early testing,
  - advanced testing, and
  - when released.

Pedigrees generally have two facets: a name and an origin, or source (both terms are used by breeders). The name is used to refer to a line, while the origin is valuable in tracing pedigree history.

Table 4.2 provides an example of a pedigree system for a station having one breeding season per year (pedigree IS 532 is used as an example). Note that the system in Table 4.2 uses a simple numerical notation in which the accession number becomes the pedigree.

Table 4.2: A pedigree notation system for one station with one season per year.

Year	Pedigree (IS)	Row no.	Selection operation*
1971	532	25	S(3)
1972	532-1	36	S(2)
	-2	37	D
	-3	38	A(3)
1973	532-1-1	5	D
	-1-2	6	A(2)
	532-3-1	7	D
	-3-2	8	U
	-3-3	9	D
1974	532-1-2-1	101	A(4)
	-1-2-2	102	D
	532	103	Increase

*Selection operation codes:

A(3) = Row is accepted but is not quite uniform. Three heads selected from row for head-rowing next year, bulk of seed from three heads sown in crossing block and crossed to tester parent(s).

S(2) = Row is not sufficiently uniform to be sown in crossing block. Two heads selected from row for head-rowing next year.

D = Discard.

U = Uniform; the row can be bulk harvested and sown in a crossing block and crossed to tester parent(s).

For more information, see section on procedures for taking notes, page 90 ff.

A number is added each time a selection is made; this selection number becomes part of the pedigree. Thus the pedigrees become longer with each generation. After six generations, a line might have pedigree 532-1-2-1-53. Such pedigrees are difficult to copy into field books and reports. When hybrids are made, the pedigrees become more cumbersome and require much page space.

The system could be modified to carry only the selection number of the previous generation. The complete pedigree including all selection numbers could be reconstructed by tracing back through breeding records. To do this, it is necessary to add an "origin." The first digits of the origin denote the previous season, while subsequent digits denote row number in that season (Table 4.3).

Nomenclature in such systems requires that the origin becomes a part of the pedigree; i.e., the origin is required to establish the pedigree; this must be maintained as carefully as the pedigree name.

The system is complicated slightly if more than one season is used at the station. In this case, selection is frequently done in the main season, and some nonselecting operation is done in the off-season—such as a crossing block to make hybrid seed, or advancing F_1s to F_2s (Table 4.4).

It is assumed that entries from the cross would go into hybrid yield trials; the origin being 72W 1350 x 72W 1097 in the 73S trials, and 73W 1600 x 73W 1065 in the 74S trials. Note that the 72W or 73W can be typed as part of the column head and that only the

Table 4.3: A different pedigree system for one station with one season per year.

Year	Origin	Pedigree	Row no.	Selection operation*
1971	Acc.IS 532	IS 532	25	S(3)
1972	71-25	532-1	36	S(2)
	25	-2	37	D
	25	-3	38	A(3)
1973	72-36	32-1	5	D
	36	-2	6	A(2)
	38	-1	7	D
	38	-2	8	U
	38	-3	9	D
1974	73- 6	532-1	101	A(4)
	6	-2	102	D
	8	532	103	Increase

*See Table 4.2 for explanation of selection operation codes.

numbers 1350 x 1097 or 1600 x 1605 would appear in the column.

This is a slightly different system in which the pedigree does not change from one generation to the next, because selection numbers are associated with the origin rather than the pedigree. A complete pedigree would be IS 532-71S 25-1. A disadvantage is that all sister lines become uniform (i.e., IS 532-1, IS 532-2S; or the name can be changed, assigning an experimental number: SPV 25—Sorghum Preliminary Variety).

Note that the seasonal difference is indicated by adding a letter to the origin. Some confusion can result when writing both numerals and letters (i.e., 5 and S, 1 and I, C or G and 6). To reduce confusion, two numerals have been used to indicate the year rather than one. The symbol 71S might be a bit clearer than the symbol 1S, which could be confused with IS. Thus the letter always follows two numerals; hence a poorly written letter S should not be confused with a 5, because it is in the third position and thus would always be a letter.

As a breeding procedure, seeds of the three selections in 73S 38 would be bulked to sow the crossing block in 73W. This has been considered satisfactory for preliminary test evaluation. Note that the nursery and crossing block would be organized separately and numbered so that no two plots in the same season are the same (i.e., nursery row numbers are less than 1000 and crossing block numbers are greater than 1000).

If an accession is highly heterogeneous, selections may be made during both seasons. The breeding record would then appear as presented in Table 4.5.

More than one location may be involved in a coordinated or cooperative breeding program and a uniform pedigree system may be useful. In cases of this

Table 4.4: A pedigree system for one station with more than one season per year.

Season	Origin	Pedigree (IS)	Row no.	Operation
				Selection operation#
1971S*	Acc. IS 532	532	25	S(3)
1972S	71S 25-1	532	36	S(2)
Nursery	-2	532	37	D
	-3	532	38	A(3)
				Pollinating instruction
1972W*	72S 38-SB	532	1097	On 1350 (20)***
Crossing block		CK60A	1350	
				Selection operation
1973S	72S 36-1	532	5	D
Nursery	-2	532	6	S(2)
	38-1	532	7	D
	-2	532	8	U
	-3	532	9	D
Yield trials	72W 1350 x 1097	CK60A x IS532	106	
				Pollinating instruction
1973W	73S 8-SB	532	1065	On 1600 (20)
Crossing block		CK60A	1600	
				Selection operation
1974S	73S 6-1	532	101	A(4)
Nursery	-2	532	102	D
	8	532-1	103	Increase
Yield trials	73W 1600 x 1065	CK60A x IS532	251	

\# See table 4.2 for explanation of selection operation codes.
* S = Summer (June to July sowing); W = Winter (January to February sowing).
** SB = Select bulk - i.e., bulk of selected heads in a row.
*** (20) = indicates that 20 heads of CK60A are to be crossed by the entry IS 532.

Table 4.5: A pedigree notation where selections are made in two seasons per year.*

Year	Origin	Pedigree (IS)	Row no.	Operation
				Selection operation
1972S	71S 25-1	532	36	S(2)
	-2	532	37	D
	-3	532	38	A(3)
1972W	72S 36-1	532	45	D
Nursery	-2	532	46	S(2)
	38-1	532	47	D
	-2	532	48	A(4)
	-3	532	49	D
				Pollinating instruction
1972W	72S 38-SB	532	1097	Cross to 1500(20)
Crossing block		CK60	1500	
				Selection operation
1973S	72W 46-1	532	5	D
	-2	532	6	A(2)
	48-1	532	7	D
	-2	532	8	U
	-3	532	9	D
	-4	532	10	D
	etc.			

*See Tables 4.2 and 4.4 for explanation of codes used.

kind, the pedigree system must be changed to include a local designation. For example:

TA = Tel Amara	Sd = Sids
Kf = Kfardan	Sh = Shandaweel
Ba = Bahteem	Iz = Izmir
Ma = Mallawi	WM = Wad Medani

One of these stations might be used as an off-season location for another—for example, Wad Medani (15° latitude) could serve as a winter-season location for the cooperative program. The movement of seeds between locations could be traced using the location designation as part of the origin; i.e., WM72W. Note that this is written as letter numeral letter, which serves to separate similar symbols (letters, numerals) with different meanings. The origin column in the above example might then appear as presented in Table 4.6.

The pedigree, row, and operations columns would be the same as in Table 4.5. A complete pedigree would be IS 532 WM72W 46-1.

Within a country or within a region, a common pedigree system is useful in developing closer cooperation (i.e., the pedigree has the same meaning for those working at all locations). Often there is a problem in establishing a workable system for the participating stations. If each station receives accessions independently of the others and assigns its own accession numbers, then a common system is not possible.

Table 4.6: A pedigree notation where more than one station is involved.

Location	Origin	Row no.
Tel Amara 72 Nursery	71TA 25-1	36
	-2	37
	-3	38
Wad Medani 72 Winter	72TA 36-1	45
	-2	46
	38-1	47
	-2	48
	-3	49
Tel Amara 73 Nursery	WM72W 46-1	5
	-2	6
	etc.	

Frequently, within a country, there is coordination of research on a crop at various relevant experiment stations. If one station serves as a coordinating station, it can act as a clearing house for accessions and assign a number that would remain uniform within the system. If there is no system of coordination, then a block of numbers might be assigned to each location; for example, 1 to 2000 to Shandaweel, 2001 to 4000 to Sids, and 4001 to 6000 to Mallawi. The first system is preferred because it provides a workable mechanism to prevent different code numbers from being assigned to the same accession. This system is facilitated if the country has a plant-introduction program. New entries can be sent by the introduction service to the coordinating center where program accession numbers can be assigned before sending the seeds to the requesting station. The second system is workable if, after a station has assigned an accession number, the number does not change when moved to another station within the system. If this procedure is followed, the only time an accession may have more than one accession number is when two stations request the same entry.

In either system, there are two possibilities of coding—in both the number remains constant, but the prefix may be for the country (i.e., Eg. for Egypt) or for a station (i.e., Sh for Shandaweel, Sd for Sids, Ma for Mallawi). Station identification is carried as part of the origin, so it is not needed on the pedigree. It is recommended that country-wide notation (such as "Eg") be encouraged; this would tend to strengthen cooperative attitudes.

Examples of these systems are shown in Tables 4.7(a) and 4.7(b).

The system of retaining station symbols can be used while a line is being developed and evaluated; then a country symbol can be added when a line has reached uniformity, or enters regional trials, or is released.

If accession numbers cannot be controlled within a program, a similar system of pedigree notation can be followed if station symbols are used with accession numbers. For example, Sh 532 and Sd 532 have the same format and will appear the same in the records, but these entries would have different accession pedigrees. This system would work only if the breeders involved agreed that these pedigrees will not be changed as they are moved within the project (i.e., Sh 532 would retain this pedigree whether sown at Shandaweel, Sids, or Mallawi). While this system is easy to manage, it loses the simplicity of the one accession number representing one pedigree within a cooperative project.

Such a system could be useful in a regional program that includes several countries.

Entries in the world collection of sorghum have been assigned "IS" numbers. Just as established pedigree names are not changed, the IS number should not change. This practice would prove useful throughout the world as many breeders use the collection. Significantly, in the conversion program of the USDA and the Texas Agricultural Experiment Station, the IS prefix and number are retained, but a "C" is added as a suffix to indicate conversion (i.e., "IS 532 C"). Similarly, countries using the NES

Table 4.7a: Examples where accession numbers for a country program are assigned at a main station using a prefix denoting country.

Year	Origin	Pedigree	Row no.	Selection operation*
71 Sh	Acc. 504	Eg 504	25	S(3)
72 Sh	71Sh 25-1	504	36	S(2)
	-2	504	37	D
	-3	504	38	S(3)

Assume that the breeder at Sids requests the selections from row 36; then in 1973 his pedigree record would appear as follows:

73 Sd	72Sh 36-1	Eg 504	45	S(3)
	-2	504	46	D
74 Sd	73Sd 45-1	504	47	S(1)
	-2	504	48	D
	-3	504	49	S(2)

*See Table 4.2 for selection operation codes.

Table 4.7b: Examples of the system where each station assigns its own prefix and has a block of accession numbers.

Year	Origin	Pedigree	Row no.	Selection operation*
71 Sh	Acc. 504	Sh 504	25	S(3)
72 Sh	71Sh 25-1	504	36	S(2)
	-2	504	37	D
	-3	504	38	S(3)

Assume that the breeder at Sids requests the selections from row 36; then in 1973 his pedigree record would appear as follows:

73 Sd	72Sh 36-1	Sh 504	45	S(3)
	-2	504	46	D

During the same year selections from Sids would appear as follows:

	72Sd 105-1	Sd 2351	47	S(2)
	-2	2351	48	D
	-3	2351	49	S(1)
74 Sd	73Sd 45-1	Sh 504	101	S(4)
	-2	504	102	D
	-3	504	103	D
	47-1	Sd 2351	104	S(2)
	-2	2351	105	S(1)
	49	2351	106	D

*See Table 4.2 for selection operation codes.
Note that the Shandaweel symbol "Sh" remains as part of the pedigree for generation after generation, while the "Sh" symbol appears in the origin column only in the records for Sids in 1973.

(Near East Sorghum) notation might use this useful notation, rather than assign new symbols.

Based on these suggestions, the records at Sids might appear as shown in Table 4.8.

Such a system is not complicated; breeders using entries with regional or international notation must simply give precedence to that nomenclature over their own, in the interest of more effective cooperation.

The nomenclature systems so far described are for a pedigree system of breeding. Eventually, the head rows will become uniform, and individual selections within the nursery row will stop: the selection operation becomes a "bulk harvest," and the origin continues to be the previous year's plot number. At this point, the line can be carried forward using the same pedigree. The pollinator parents of CSH-1 and CSH-2, IS 84 and IS 3691, respectively, have been maintained using the original nomenclature. If several sister lines of IS 84 should become uniform they could be differentiated by the origin. A uniform line would not be carried forward for any length of time; it would be released as a line or as a parent in a hybrid (or would be dropped). (Names for released lines and hybrids are discussed in a later section.)

In summary, the advantages of such a system are:

- There are no long pedigrees.
- Numerals and letters are separated where meaning changes, and each numeral or letter falls at a specific spot so confusion from poorly written characters is avoided. Pedigree history can be

Table 4.8: A pedigree system involving lines with well-established names.

Year	Origin	Pedigree	Row no.	Selection operation*
73 Sd	72Sh 36-1	Eg 504	45	S(3)
	-2	504	46	D
	72Sd 101-1	IS 532	47	D
	-2	532	48	S(2)
	-3	532	49	D
	105-1	NES 4055	50	D
	-2	4055	51	S(1)
	106	Plainsman	52	Bulk
74 Sd	73Sd 45-1	Eg 504	141	D
	-2	504	142	S(3)
	-3	504	143	D
	48-1	IS 532	144	D
	-2	532	145	S(2)
	51	NES 405	146	S(3)
	52	Plainsman	147	Bulk

*See Table 4.2 for selection operation codes.

readily traced through seasons and locations. Well-known pedigrees are maintained. Selections from the same entry in the coordinated system keep the same identity at any location in the system, thus all breeders in a coordinated program make the same pedigree associations. The origin is part of the pedigree.

Nomenclature When Crossing Is Involved

Crosses are made: (a) for backcrossing, (b) to develop a source from which to select new lines, and (c) to make hybrids for direct evaluation. Pedigree considerations for each of these purposes are presented in Tables 4.9 to 4.12 (additional information about sowing and operating a crossing block begins on page 93 ff.).

Backcrossing

This breeding procedure is used to transfer a desirable trait from a source (nonrecurrent) line to required (recurrent) lines that do not have the trait.

Backcrossing to Make Male-sterile Seed Parents: An important backcrossing program in sorghum is the development of new pollen-sterile lines to be used as seed parents in hybrid programs. By backcrossing, it is possible to recover the phenotype of the recurrent parent, but as a male-sterile. The backcrossing process is illustrated in Table 4.9 (a more detailed discussion begins on page 115). The use of an off-season nursery would double the speed of the backcrossing program.

It is assumed in the example (Table 4.9) that only one nonrecurrent source is being used—i.e., CK 60A. If more than one source is used, it is possible to

Table 4.9: Backcrossing to make male-sterile seed parents.

Station		Origin	Pedigree	Row no.	Pollinating instructions	Selection operation#
Tel Amara 1971S			IS 534*	37	Self and on 38**	S(3)
			CK60A	38	x's 37***	S(3)
Wad Medani 1971W	TA71S	37-1	IS 534	62	Self and on 63	D
		38-1 x 37-1	CK60A x IS 534	63	x's 62	D
		37-2	IS 534	64	Self and on 65	S(2)
		38-2 x 37-2	CK60A x IS 534	65	x's 64	S(2)
		37-3	IS 534	66	Self and on 67	S(1)
		38-3 x 37-3	CK60A x IS 534	67	x's 66	S(1)
Tel Amara 1972S	WM71W	64-1	IS 534	5	Self and on 6	S(3)
		65-1 x 64-1	F_1 x IS 534†	6	x's 5	S(3)
		64-2	IS 534	7	Self and on 8	D
		65-2 x 64-2	F_1 x IS 534	8	x's 7	D
		66-1	IS 534	9	Self and on 10	S(2)
		67-1 x 66-1	F_1 x IS 534	10	x's 9	S(2)
Wad Medani 1972W	TA72S	5-1	IS 534	42	Self and on 43	S(1)
		5-1 x 6-1	BC_1 x IS 534†	43	x's 42	S(1)
		5-2	IS 534	44	Self and on 45	D
		5-2 x 6-2	BC_1 x IS 534	45	x's 44	D
		5-3	IS 534	46	Self and on 47	S(3)
		5-3 x 6-3	BC_1 x 534	47	x's 46	S(3)
		9-1	IS 534	48	Self and on 49	D
		9-1 x 10-1	BC_1 x IS 534	49	x's 48	D
		9-2	IS 534	50	Self and on 51	S(2)
		9-2 x 10-2	BC_1 x IS 534	51	x's 50	S(2)

\# See Table 4.2 for selection operation codes.
* Assume that it is known that IS 534 is nonrestoring when crossed onto male-sterile Combine Kafir 60 (A line).
** Self and on = pollen is placed on the same head from which it was collected and on a head in a different row.
*** x's = pollen is brought in from another row (for example, row number 37) to make a cross.
† F_1 = CK60A x IS 534; BC_1 = (CK60A x IS 534) x IS 534, etc.

use some notation such as superscripts to avoid writing long pedigrees. For example:

with CK60A, use BC_1^1, with IS 3657A use BC_1^2, and with Martin A use BC_1^3.

It would be necessary only to clearly define the meaning of these symbols in the field book; such definition of symbols is extremely important and frequently overlooked.

After the type is recovered with the male-sterile background, some symbols are required to denote this event. The best symbols are IS 534A for the male-sterile and IS 534B for the maintainer. If more than one sterile is derived, then IS 534A-1, IS 534B-1 and IS 534A-2, IS 534B-2, etc., could be used. (Note that by employing the operational symbols in the backcrossing program, selection for agronomic improvement goes along simultaneously with the recovery of male-sterility.)

Backcrossing to Transfer a Single Recessive Trait: Backcrossing may also be used to transfer, or partially transfer, characteristics such as high lysine and disease or insect resistance, etc. If the factor is simply inherited, the recurrent phenotype can be effectively recovered with the required character incorporated. Specific conditions would determine the need for a change in pedigree notation. If a line were converted to carry high lysine, the new notation might be IS 534 hl, (i.e., the gene symbol would be carried). If resistance to disease were to be incorporated, the change might be of sufficient commercial interest to involve a new name. If a long-standing variety were improved by adding resistance to a disease, it might be desirable to make only a slight modification of the pedigree (i.e., IS 534R as a name, but elsewhere on the bag of seed, descriptive information could mention the disease to which it was resistant).

A recessive trait is not expressed in an F_1; hence, periodic selfing is required to expose recessive characters during the backcrossing process. Assume a recessive trait "a"; then the F_1 is Aa and the first backcross would be Aa x AA with progeny ½ AA to ½ Aa. If this progeny is self-pollinated, the heterozygote would segregate 1 AA : 2 Aa : 1 aa, and there would be 4 AA individuals from selfing the homozygous class. The F_2 progeny would be 5 AA : 2 Aa : 1 aa (⅛ of the progeny would have the recessive phenotype). The second backcross would then be aa x AA, and the process would be repeated.

Assuming no selective operation while backcrossing (so that any operation can be done in any season), the records would appear as presented in Table 4.10. Assume that NES 601 and 654 are the recurrent AA parents and that IS 11758 is the nonrecurrent parent; also assume that the station involved is Eskisehir (Es) in Turkey.

If more than one nonrecurrent parent were involved with the same recurrent parents, superscripts could be used on the F_1, BC_1, etc. Assume that IS 11758 and IS 11167 are both nonrecurrent parents; then the pedigrees in Es 75 would be F_1 (11758) x NES 601 and F_1 (11167) x NES 601. A code could also be employed:

F_1^1 x NES 601 and F_1^2 xNES 601,
when IS 11758 and IS 11167 are used.

The pedigree in Es would be:
601 (BC_1^1) F_2 x NES 601 and
601 (BC_1^2) F_2 x NES 601.

It would be important to note the actual pedigree of the superscripts 1, 2, etc., in the field books, so that the pedigree record is complete. (IS 11758 and IS 11167 are sources of high lysine: hl/hl.)

If the character under consideration were controlled by many genes (quantitative), the number of backcrosses would be limited and a new line would have to be selected from the cross. It may be that only one or two backcrosses are possible before the expression of the character to be transferred becomes too weak or diluted to justify further backcrossing; thus selfing must begin. Under such circumstances, the pedigree of the new line(s) would change. The backcrossing portion essentially involves crossing two lines with the idea of recovering one line that would appear much as it appeared initially. After selfing has begun, the aim is to derive a new line, i.e., something different from either of the parents. A pedigree change might then be required when the selfing process begins.

Crossing as a Source from Which to Select New Lines

In handling lines arising from crosses, it is suggested that each cross be assigned a new accession number; the process could then proceed as in the previous examples. For example, assume a cross between Eg 504 and Eg 2351 and Sh 504 and Sd 2351 at Sids. The cross was made at Sids 1973, and the F_1 was advanced to F_2 in the winter nursery at Wad Medani. A new accession number, Sd 3015, was assigned to the cross Sh 504 x Sd 2351. The F_2 was grown at Sids in 1974 and selection made for head-to-row planting in 1975. To avoid a rapid increase in new numbers, it is possible to assign a number only to those crosses from which one or more selections were made in the F_2 generation.

Table 4.10: Backcrossing to transfer a single recessive trait.

Season	Genetics	Origin	Pedigree	Row no.	Pollinating instruction
74Es	P_1 {+/+}	73Ta 205	NES 601	26	x's and on 28(3)*
	P_2 {+/+}	73Es 502	654	27	x's and on 28(3)
	P_3 {hl/hl}	73WM 405	IS 11758	28	x's and on 26(3), 27(3)
WM74W	F_1 {+/hl}	74Es 26 x 28	NES 601 x IS 11758	101	x's and on 102(3)
	P_1 {+/+}	26	601	102	x's and on 101(3),⊗(4)**
	F_1 {+/hl}	27 x 28	NES 654 x IS 11758	103	x's and on 104(3)
	P_2 {+/+}	27	654	104	x's and on 103(3),⊗(4)
75Es	BC_1 {+/+:+/hl}	WM74W 101 x 102	NES 601(BC_1)	95	⊗(20) Select shrunken seeds
	BC_1 {+/+:+/hl}	103 x 104	654(BC_1)	96	⊗(20) "
WM75W	(BC_1)F_2 {hl/hl}	75Es 95	NES 601(BC_1)F_2	250	x's and on 251(3)
	P_1 {+/+}	74Es 102	601	251	x's and on 250(3),⊗(4)
	(BC_1)F_2 {hl/hl}	75Es 96	654(BC_1)F_2	252	x's and on 253(3)
	P_2 {+/+}	74Es 104	654	253	x's and on 252(3),⊗(4)
76Es	BC_2 {+/hl}	WM75W 250 x 251	NES 601(BC_1)F_2x601	312	x's and on 313(3)
	P_1 {+/+}	251	601	313	x's and on 312(3),⊗(4)
	BC_2 {+/hl}	252 x 253	654(BC_1)F_2x601	314	x's and on 315(3)
	P_2 {+/+}	253	654	315	x's and on 314(3),⊗(4)
WM76W	BC_3 {+/+:+/hl}	76Es 312 x 313	601(BC_3)	275	⊗(20)
	BC_3 {+/+:+/hl}	314 x 315	654(BC_3)	276	⊗(20)
77Es	(BC_3)F_2 {4+/+; 1+/+:2+/hl: 1 hl/hl}	WM76W 275	NES 601(BC_3)F_2	402	⊗(100)
	(BC_3)F_2	276	654(BC_3)F_2	403	⊗(100)
Hign lysine segregates would be identified by chemical analysis					
WM77W	(BC_3)F_3 {hl/hl}	77Es 402	NES 601(BC_3)F_3	512	x's and on 513(3)
	P_1 {+/+}	76Es 313	601	513	x's and on 512(3),⊗(4)
	(BC_3)F_3 {hl/hl}	77Es 403	654(BC_3)F_3	514	x's and on 515(3)
	P_2 {+/+}	76Es 315	654	515	x's and on 514(3),⊗(4)
78Es	BC_4 {+/hl}	WM77W 512 x 513	NES 601(BC_4)	375	x's and on 376(3)
	P_1 {+/+}	513	601	376	x's and on 375(3),⊗(4)
	BC_4 {+/hl}	514 x 515	654(BC_4)	377	x's and on 378(3)
WM78W	BC_5 {+/+:+/hl}	78Es 375 x 376	601 (BC_5)	65	⊗(20)
	BC_5 {+/+:+/hl}	377 x 378	654(BC_5)	66	⊗(20)

* x's and on 28(3) indicates that pollen is brought from three plants in row 28 and placed on three heads in row 26 and that pollen from three plants in row 26 is placed on three heads in row 28.

** ⊗ is a symbol used to define self pollination; ⊗(4) indicates that four self pollinations should be made in the row.

Note that the seed formed on half of the BC_1 plants will be {+/+} and on the other half will segregate {+/+: +/hl}. The high-lysine gene (hl) appears to be associated pleiotropically with shrunken seeds. Assume that the shrunken seeds are good high-lysine types and can be selected by visual inspection.

Suppose that it is desired to select high-lysine segregates from plants homozygous for this trait. Seeds from the BC_1 are sown; seeds on the heads of some of the plants will be shrunken. These shrunken seeds are sown and at flowering time can be crossed by the +/+ parent, making the second backcross.

The high-lysine segregates could again be identified as shrunken seeds on segregating heads. This process is normally carried on for five to eight backcrosses. After this much backcrossing the nonrecurrent parent, NES 601(BC_5 to $_8$) F_2 {hl/hl}, is usually phenotypically similar enough to the recurrent parent, NES 601, that backcrossing can stop. At this time the recurrent parent could be given the pedigree name NES 601 hl, using the gene symbol to indicate high lysine.

The record would appear as presented in Table 4.11.

Crossing as Part of a Hybrid Program

If hybrids are made for evaluation as part of a program to develop them for farmer use, then it is suggested that new number not be assigned, and that the hybrid be identified by parental pedigrees. This will help the breeder keep track of parentage and is probably a more useful system. The record would appear as shown in Table 4.12. These hybrids are an end in themselves; i.e., there is no selection in advanced generations. Also new hybrid seed must be obtained when the existing supply runs out. Maintaining the pedigrees as indicated is simple enough that assignment of a hybrid number is not considered to be advantageous. It is suggested that both B and R lines are testcrossed beginning in the F_4 generation (see page 116 ff.).

Nomenclature for Lines and Hybrids to be Released

By the time a line has become uniform, it has been (or will be) evaluated in yield tests as a line, or as a parent in a hybrid. If the line is advanced in the breeding program because of promising yield results at a station, it should soon be involved in statewide or regional testing. The yield evaluation on a state basis is usually at the discretion of the plant breeder. The decision for regional yield testing of a line (across state or country boundaries) usually depends on a broader group consideration. It should be a matter of prestige for a line to be

Table 4.11: A pedigree system for lines selected from crosses.*

Year	Origin	Pedigree	Row no.	Operation
				Pollinating instruction
73Sd	72Sh 36	Sh 504	105	on or x's 106(3)
	72Sd 105	Sd 2351	106	
WM73W	73Sd 105 x 106	Sd 3015	93	Self pollinate
				Selection operation
74Sd	WM73W 93	Sd 3015	233	S(5)
75Sd	74Sd 233-1	3015	102	S(2)
	-2	3015	103	S(3)
	-3	3015	104	D
	-4	3015	105	S(1)
	-5	3015	106	S(2)

*See previous tables for explanation of symbols.

Table 4.12: A pedigree system for developing F_1 hybrids for farmer use.

Year	Origin	Pedigree	Row no.	Pollinating instruction
73Sd	Acc.	CK60A	25	x's 105(10), 106(10)
	72Sh 36	Eg 504	105	on 25(10)
	72Sd 105	Eg 2351	106	on 25(10)
			Entry no.	Plot no.
74Sd	73Sd 25 x 105	CK60 x Eg 504	7	1
Yield	x 106	x Eg 2351	12	2
Trial				

involved in regional testing. To place an entry in regional trials, a plant breeder should be able to present justification to a group representing the various districts, provinces, states, or countries of the region. This group usually is composed of plant breeders from the region who meet annually at a workers' conference. Justification for entry in regional testing usually involves the presentation of supporting yield trial results indicating superiority in station or statewide testing and availability of sufficient seeds for inclusion in the regional testing program.

Testing, statewide or regional, probably would continue for 2 or 3 years, although it may take only one season for obviously outstanding types. A decision as to whether to continue the testing of a line should be made after each testing season. (This decision is made by the group at its workers' conference in the case of regional testing.) Entries passing successfully through state or regional trials would then be considered for release, with appropriate nomenclature for released lines and hybrids.

A hybrid designation should be simple—generally a word of not more than two syllables that is easily spelled and pronounced. Designations often attempt to indicate regional or seasonal adaptation. For example, the Coordinated Maize Improvement Scheme (India) has chosen the names Ganga and Deccan to show the broad regional areas of maize adaptation. In addition, color of endosperm is identified by odd numbers for yellow and even numbers for white hybrids. Within the regional designation, maturity is broadly indicated with a one-digit number used for early hybrids and a three-digit number for late maturing hybrids. Sometimes the region of adaptation indicated by name may lead to difficulties. (For example, Ganga Hybrid Makka No.3: the designation Ganga suggests that it should be adapted to the Gangetic plain; however, the hybrid might well find adaptation to other regions where an early maize hybrid is required.)

If a regional designation is desired, it should be a broad general region. Maize hybrids released by the Southern Corn Improvement Conference of the USA carry the designation "Dixie." In the case of sorghum hybrids, breeders have adopted the designation RS (Regional Sorghum), with the numbers indicating different hybrids; RS 630, etc. The sorghum workers in India have used the letters CSH to designate released hybrids. The "C" stands for "Coordinated" and indicates regional adaptation (as well as giving credit to the regional effort); "S" stands for "Sorghum" and identifies the crop; "H" stands for "Hybrid" and was included as a promotional "catch" word. The first hybrid of sorghum was released in India in October 1964. Since the hybrid was a new innovation, it made a good vehicle to promote better management practices, better soil fertility, plant protection, irrigation management, weed control, etc. The idea was to release a hybrid plus a package of practices. After the letters CSH, a number was assigned in order of release (CSH-1, CSH-2, etc.).

A series of numbers to designate adaptation and to index hybrids into classes can be useful—such a series might be:

100 — early
200 — medium
300 — midseason
400 — medium-late
500 — late

Names of sorghum cultivars (i.e., cultivated varieties) released in India have frequently carried a station identification notation—for example, Co for Coimbatore and N for Nandyal. Varietal names have also been used (for example M 35-1, where the M comes from the name Maldandi, and they are commonly used in the United States) Combine Kafir 60, Early Hegari, Ryer Milo, etc. Inbred lines used as parents in hybrids of corn in the United States may carry state names (such as Oh43, where Oh stands for Ohio); or certain letters may be used by particular states, such as H52 by Indiana and B14 by Iowa, so that those letters represent those states.

Some lines and hybrids will be considered by state variety release committees and some will be released for a region. Pedigree notation will vary—for example, the nomenclature CSH-1 has been used for a regionally released hybrid in India. The parents are Combine Kafir 60 and IS 84; this nomenclature for the parents is in current use. It would not be desirable to rename Combine Kafir 60, because it is a released line of the Texas Agricultural Experiment Station (USA). The pedigree IS 84 was assigned as an accession number to an introduction of an early generation breeding stock. Other notation might be given to this line, for example, CS-1 for Coordinated Sorghum line number 1. It could be given station identification, for example, P-1 or P184 after Pusa Institute (Indian Agricultural Research Institute). It is suggested that parental lines of hybrids released in a region be given a regionally identifying nomenclature (CS-1) and that regionally released varieties also be given a regional name.

Ordinary or hybrid cultivars and parent lines released for regional use should carry regional

identification. These materials frequently carry station or state identification that may have strong associations—both favorable and unfavorable—for people in other areas. (Farmers, politicians, administrators, etc., seem to consciously or unconsciously favor local names—an Indiana name in Indiana rather than an Illinois name, or an Andhra name in Andhra Pradesh rather than a Maharashtra name, even though the Illinois or Maharashtra material may be superior). Thus the use of station and state names may have an adverse impact on the most effective use of the best material.

Some naming systems do not involve station or state names. The use of H and B notation for inbred lines of corn in Indiana and Iowa have no relationship to the names Indiana and Iowa, respectively. The name Combine Kafir 60 has little relationship to the state of Texas (where it has been released). Sweet-corn hybrids in the USA have names such as Indian Chief and Golden Cross Bantam. The name Ranjit has been assigned to a hybrid maize; Ranjit is the name of an Indian hero of bygone days. Generally descriptive "catch" words are useful as names and helpful in regional acceptability of a line or hybrid.

Use of location and state names helps acknowledge the originating researchers; however, it is suggested that the disadvantages outweigh the advantages, and that other names should be sought. Proper acknowledgment can be obtained through some form of publication and through widespread use of the line or hybrid.

Breeding Objectives and Procedures

Pedigree Breeding

Pollination Procedures

Pollination in a primarily self-pollinated crop such as sorghum frequently amounts to no more than putting a bag on the head prior to flowering in order to ensure that no cross-pollination takes place; however, crossing is a bit more complicated. Procedures are discussed here for making such crosses in large numbers.

Highly heterogeneous materials may enter a breeding program either from collections or from segregating populations. Frequently, introduced breeding stocks vary because they are an early generation from a cross and/or because lines uniform in the originating area are variable in expression in a new environment. Outcrossing in some sorghums commonly varies from 1 to 10%; in other sorghums it varies from 30 to 60%—the variation depending largely on head compactness (the open-headed grassy types being more prone to cross pollination). However, sorghum is generally considered to be a self-pollinating crop, with less than 10% cross-pollination. When highly variable stocks are grown, no head bagging need be attempted. Thousands of heads could be bagged, involving much time and effort, only to have 95% of the entries discarded at maturity. For a generation or two, it is easier to rogue "off-type" plants from an occasional cross, than to head bag. Thus, it is best not to place head bags and to select from a much greater number of entries; selection is the important function when variation is great.

Selected plants from various nurseries or populations will eventually become uniform, and if they perform well, may be entered in yield trials. When the requirement is to attain and maintain uniformity of good breeding stocks, head bagging becomes efficient. Once the decision to bag heads has been made, all heads in a row should be covered. There are several reasons for this recommendation: selection of plants within a plot at the time of flowering is not effective (the author once tried selecting at flowering time and his results were only 20% correct when compared to selections made at maturity). Heads under bags frequently do not develop quite as well as those that are not bagged; if only a portion of a row is bagged, there is a tendency to select unbagged plants at maturity because they look better. Bagging of all heads eliminates these problems.

Only the nonflowering portion of a head should be bagged. If a head has already begun to flower, the flowering portion should be cut off. This should be held to a minimum, especially where plant selections will be made within a plot. There is a natural tendency to discard if only a portion of a head remains on the plant.

Head bagging can be an effective means of controlling midge. Midge lays its egg in the floret just prior to flowering. If head bagging is done early, midge control can be 100%. If midge is a serious threat, it may be useful to head bag segregating populations.

Head bags should be placed quickly. One trained worker with one or two helpers can form an effective team. The trained worker can place the head bag on the plant and the helpers can close and staple the bag shut. The top leaf of the plant is usually removed prior to placing the pollinating bag. If the number of

trained people are few compared to available helpers, the trained worker can remove the top leaf, while one helper places the bag and two others staple. (Using this procedure in India, three trained people and a crew of helpers have placed 12000 bags in 1 day.) In this procedure, a few selected heads may be missed; to minimize this error, the crew should not become too widely separated. The number of heads covered is so great, compared to other techniques, that the loss of a few heads is well compensated for. (Frequently, between 30000 and 50000 bags were used per nursery in the program in India. When the world collection is increased, about 100000 bags are used.)

Pedigree Selection

Pedigree selection is a head-to-row process. A head is taken from a selected plant within a plot. Seed from this head is sown in a nursery row the following year, and the process is repeated until the line is discarded or becomes uniform. When the line is uniform, it is bulk harvested.

Varieties from a pedigree breeding process should be included in yield trials after obtaining reasonable uniformity. It is a waste of time and facilities to delay yield testing until uniformity has been achieved. For example, testing can begin in the F_4 or F_5 generation.

The selection pressure that can be applied depends on how well a nursery is grown—the better the crop, the better the selection opportunity. More entries are usually taken if the nursery is poor and cannot be properly evaluated. The better the nursery, the faster the progress from breeding. Generally, a nursery in which pedigree selection is being done will have 800 to 1500 entries. The nursery usually is not replicated, and frequently plots are of one 4- to 5-m-long row. (Notes to be taken are described in the section on note-taking, but generally it is recommended that the breeder concentrate on larger numbers of entries from which he can select, rather than to obtain many detailed notes on fewer entries.)

Procedures for Taking Notes

Notes taken in a nursery will vary with the kind of nursery and the objectives. A nursery that is highly heterogeneous (composed of unselected collections) will probably require few notes. The only note required in an F_2 population from diverse parents may be an indication of the selection made; i.e., the only real operation in such a nursery would be plant selection. The notes in a nursery of unselected collections need be only selection notes indicating which entries are to be propagated and which are to be discarded. As selection proceeds, a few more notes are required: seedling vigor, days to 50% flowering, plant height, lodging (if serious), and any severe attack by insect or disease, etc. If nurseries are grown for a special purpose—for example, classification—then relevant characters must be measured.

Time can frequently be saved by the procedure used in taking notes. Notes on days to 50% flowering should be taken every 2 or 3 days during the flowering period. A visual estimate of when the row is 50% flowered is satisfactory. Plant height is a measure of the distance from the ground to the tip of the panicle. One "eyeball" average in a plot is satisfactory for most practical uses. The measuring of 5 or 10 plants, and then averaging, provides an accuracy beyond that normally required for the use made of such data. Lodging can be estimated. It is easy to estimate the difference between 0 and 10% lodging, but not between 50 and 60%; however, a scale can be established that is easier to use in making visual estimates (0 to 10%, 10 to 25%, 25 to 50%, 50 to 75%, 75 to 90%, 90 to 100%, for example). Estimates using such a grouping are not difficult, and for general breeding purposes are sufficiently accurate. Seedling vigor, disease, and insect data can be estimated by using a numerical score. Such scores are usually 1 to 5, with 1 being the most resistant and 5 the least resistant.

Selection of which entries to propagate and to discard from a nursery can be done by analyzing an array of data. Or the decision can be based primarily on familiarity with entries in the nursery throughout the season (especially by inspection of the rows at harvest time). (The author finds the second method is the best by far.) Scores used to estimate vigor have limited use; i.e., they are helpful in selection in a nursery of diverse varieties. As selection proceeds and the poor entries are discarded from a nursery, the scores tend toward an average. For example, assume that score 1 is the most vigorous and 5 the least: after several generations of selection, almost all entries will be scored 2 or 3—these data are of little use.

A set of operative symbols can be used to describe how material is to be advanced: this can be done at harvest time based on the breeder's opinion of the entry. The author has found the following system quite useful, although it has some limitations. A set of five letters is used to indicate how a nursery entry will be managed in a breeding program to develop hybrids.

The letter "U" indicates that the row is uniform and good, that it should be bulk harvested, and that seed should be sown in the off-season crossing block. The hybrid would be entered in yield trial(s) in the same season of the next year and the row sown again in the nursery.

The letter "A" indicates that the row is accepted but is not quite uniform. Individual heads are selected from the row, and a portion of seed from each head is mixed to plant a row in the off-season crossing block. The hybrid is sown in yield trial(s) in the same season of the following year, and seed from each head is sown in one row in the nursery (head-to-row).

The letter "S" indicates that the row is selected but is not sufficiently uniform to be sown in the crossing block. Individual heads are selected, and are sown head-to-row in the nursery during the same season of the following year.

The letter "R" indicates that the row should be repeated, resowing from remnant seed during the same season of the following year. This note indicates that the row was not growing properly so that its real potential could not be evaluated.

The letter "D" indicates that the row is discarded from the nursery.

The letters "S", "R", and "D" are also useful in a program for varietal improvement. Other useful symbols are "Y", indicating bulk harvest for an entry to be included in yield trials; "CB" for an entry to be included in a crossing block; "NR" indicates bulk harvest of an entry to be included in regional nurseries or yield trials; "com." indicates that the entry should be considered for inclusion in a composite. The symbol "ⓐ" means self-pollinate; the symbols, "#" or "θ" indicate sib-pollinate. Other symbols useful in a breeding program can readily be developed by the breeder to suit his own needs.

The number of heads marked "A" or "S" are indicated in parentheses after the selection letter in the field book. For example, A(5) indicates that five heads were taken from selected plants and that there will be five rows in the nursery the following year, with one row in the off-season crossing block; and that the hybrid will be in yield trials the following year. With notes on this type, the nursery and yield trials can be determined the following year. Such information facilitates putting up seed and making field books. The important thing is that selection notes are based directly on field observations, and that the note taken is operational rather than simply descriptive.

This system is effective only if good testing is carried on along with it; i.e., poor parents must be quickly dropped from the nursery, based on yield trial results, so that they are not repeat tested. Repeat testing of superior hybrids is required prior to release, so it is not inconvenient to have an A or U symbol assigned for several seasons, indicating that testing should continue. Repeat testing because no decision is made about the merit of a hybrid and its parents should be avoided. There may be instances where it is desirable to hold an A or U line in the nursery without yield testing; a symbol could be used to indicate this.

A uniform system of note-taking is very useful in a coordinated country program.

Selection

Plant breeding is both an art and a science. Much of the art in plant breeding is relevant to the selection process. It is difficult to quantify why one entry is selected and another is not. A breeder selects based on his experience, the objectives in his program, a visual impression of the entry that he is looking at; an important component of selection is subjective.

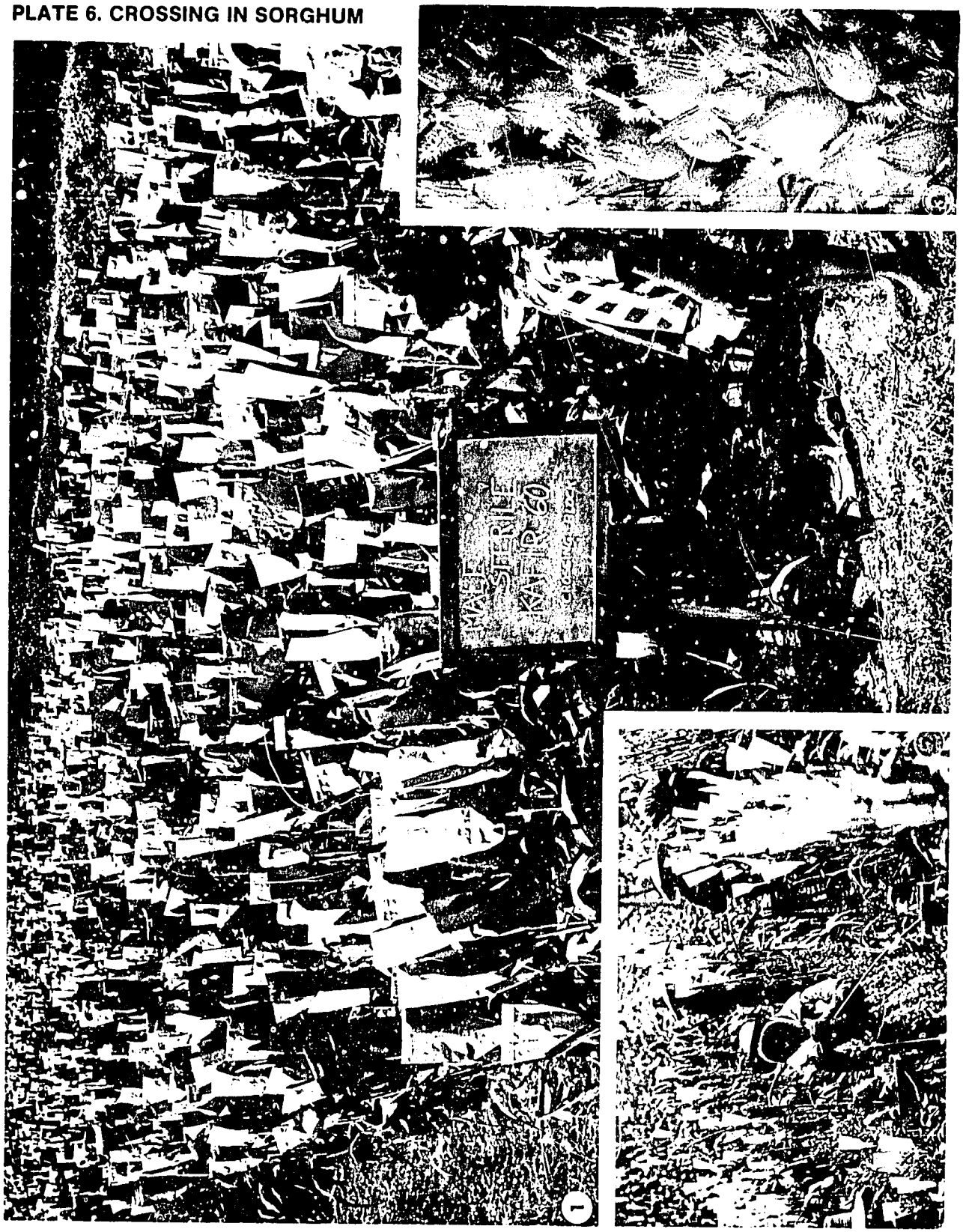
There are two aspects of selection—one is the development of elite varieties and parents for hybrids—the other is the maintenance, even increase, in the diversity of breeding stock. The first rapidly exploits variability, the second generates new variability. Both aspects are important to keep in mind while selecting.

Selection criteria will vary with location and objective. There are many traits that can be listed that are involved in selection. A breeder, almost subconsciously, integrates many of these traits when he evaluates a pedigree. Relationships are of value; i.e., more selections may be made in advanced generations from crosses where one parent is known to be a good combiner. Phenotypic traits are important—head types 2E, 3E, 3D, 4D, and 6, for example, are expected to yield more and generally combine better than head types such as 1, 2D, 5, 7, 8, and 9 (see page 180); hence selections would likely be more among the former than the latter. The following is a suggested list of traits one or any combination of which may be selected at any one time: (See also Sorghum Descriptors, Appendix 2).

General Criteria:

- high yield (fertilizer responsive)
- wide environmental adaptiveness
- disease and insect resistance
- nonlodging
- appropriate time to maturity
- good plants at reasonable population levels

PLATE 6. CROSSING IN SORGHUM



(1) Part of a crossing block in which some 15 000 cross-pollinations were made onto male-sterile plants. (2) A portion of a crossing block in which some 3000 cross-pollinations were made on hand-emasculated heads. (3) A male-sterile head in flower; there are not even rudimentary anthers on this head.

good threshability
general attractiveness
height—about 1.25 to 2.0 meters
large head size
good head exsertion
head not too compact or too grassy
head erect rather than recurved
good tillering, with heads on all culms maturing at the same time
good seed set
good seed size and number

Grain Quality:

as a food - meets preferences for color, hardness, luster, taste, storability, dough properties, etc.
as a food or feed - high in nutrients; storable (hard seeds are less attacked by weevils).
as a feed - digestible and palatable.

Plant Characteristics:

in dry areas - drought-tolerant, relatively short duration, heat tolerant.
in wet areas - resistant to grain weathering and grain mold, normal floret development on lower panicle branches (the number may be reduced and those present may be female-sterile), open heads so sunlight and air penetrate.
for forage - leafy, good tillering, thin stemmed, juicy sweet, reasonably good grain yield, palatable, digestible, low in HCN.

Other Criteria:

good ratooning
bird-resistant
tan plant color
short coraceous glumes
resistance to witchweed (*Striga*)
vigorous seedlings
cold-weather tolerant
well-developed root system
short seed dormancy period

Crossing in Sorghum

Sorghum is a perfect-flowered plant (i.e., has both sexes in the same floret); thus effective crossing involves the removal of anthers from the florets to be crossed before dehiscence. Hybridization of sorghum on a field scale is made feasible through the use of a cytoplasmic genome interaction resulting in male-sterility. There are a number of genes in sorghum that produce male-sterility. Effective use of genetic or cytoplasmic sterility makes it easier to incorporate the desired characters into the lines of interest.

Crossing between normal male-fertile lines can be accomplished by means of (1) hand emasculation or (2) treatment with hot water, or use of a plastic bag technique. The effective use of these techniques requires skill: florets can be easily damaged when hand emasculated so that they later will not set seed, or pieces of anthers may remain that result in self-pollination. The use of hot water requires that the head be soaked for the correct period of time, and at the correct temperature, so as to kill the male organs but not the female organs. Varieties respond differently to this technique; thus it may not be equally effective on all entries in a cross block.

Choosing Parents for Crossing

The number of selections that can be made in advanced generations from a cross varies with the parents in the cross; with some parents, few good plants are found in an F_2, F_3 (etc) generation for selection. Sometimes lines are used as parents because of some important trait; they may be used even though it is difficult to find good plants for selection in the segregating generations. Generally, lines can be chosen that have shown good general combining ability in test cross trials as illustrated in Table 4.13. In this example lines 2 and 4 have shown the best combining ability and might be used more extensively in crossing than lines 1, 3, and 5.

Another method is to list the parents that occur in a nursery of F_2, F_3, etc. progony and determine the number of selections made involving each parent. Suppose that we are looking at an F_2 nursery with parents 1, 2, 3, 4, 5—n; the crosses involved may be as shown in Table 4.14.

Table 4.13: Use of testcross results to select parents for crossing.

	Yield (kg/ha)					
	Lines					
Testers	1	2	3	4	5	--n
A	1503	3057	2532	4170	1875	
B	1704	3100	1908	3875	2560	
C	982	3750	2324	3545	2810	
D	1935	3270	2705	4080	2090	
Avg	1540	3294	2367	3917	2321	

Table 4.14: Crosses involved in an F_2 nursery with parents 1, 2, 3, etc.

	Parents								
Parents	1	2	3	4	5	6	7	8	--n
	Number of selections								
1		1		1	1			1	
2			2	3	2	4	1		
3					1		2	1	
4					1	4	2	2	
5						4		2	
6							3	5	
7								2	
8									
"									
"									
n									

The lines and the selections including them can be listed as follows:

	No. of times in crosses (I)	No. of selections (II)	Ratio (II/I)
1	4	4	1.0
2	6	13	2.2
3	3	6	2.0
4	6	8	1.3
5	7	11	1.6
6	5	20	4.0
7	4	10	2.5
8	6	13	2.2
"			
"			
n			

We can see from the example in Table 4.14 that the most selections were obtained from crosses where line 6 was involved and fewest where line 1 was involved. It can be concluded that line 6 was very valuable in a crossing program, that lines 2,3,7,8 were contributing, and that lines 1,4, and 5 would likely only be included in a crossing program if they had some special trait that was wanted.

Factors Influencing Time from Sowing to Flowering

Sowing Interval: If the time from sowing to flowering is known for all the lines in the crossing block, and for the location and season in which they are to be grown, then the parents from each cross can be sown in adjacent rows. Date of sowing will be adjusted for one of the parents, so that flowering will be simultaneous (the parents' *nick*). If the time from sowing to flowering is not known, each parent can be sown in one plot, adjusting the sowings to 2, 3, 4, or 5 sowing intervals, so that the desired crosses can be made. The paired-row arrangement requires more land, but is easy to operate. Sowing all the parents in one plot requires more record-keeping during the time of pollination. Either technique is satisfactory.

Photoperiod and Temperature: The time from sowing until flowering varies considerably for many varieties, depending on sowing date, crop management, latitude, and temperature. Generally speaking, flowering of different lines will occur more nearly at the same time if sowings are made while the days are getting shorter; whereas time of flowering will become more divergent if sowings are made while the day lengths are increasing. At a latitude of roughly 12° N, flowering will be more nearly simultaneous in sowings made from July to December (being closest in late November and December sowings). Flowering times will diverge in sowings made in late March and April. Some lines sown in April will remain vegetative until September. Temperature is important: sorghum grows very slowly at temperatures below 15° C; crossing at a temperature of 40° C (with low humidity) usually results in failure of seed set. In temperate zones and high elevations in the tropics, sorghum can usually be grown only in one season, while in the warm tropics it can be sown at almost any time. Temperatures between 25° and 30° C are most suitable. Crossing, especially by hand emasculation, is tedious; comfortable working temperatures allow workers to do a better job. Rain is also important; continuous rains during flowering make working conditions more difficult and cause losses of crosses. Excessive rain and humidity during the period of seed ripening can cause deterioration of the seed and loss of viability.

An ideal time for sowing a crossing block in Southeast Asia is from October through November; the temperatures are comfortable, the sequence of day length is shortening, and there is little or no rain from the period of flowering to harvest (irrigation is required). The reverse is true in the Near East, where cold winter temperatures make crop growth impossible; however, the dry summers are ideal for crossing.

To achieve a nick between parents to be crossed, it is frequently necessary to sow the two parents at different times. However, if the difference in flower-

ing dates between two parents is 6 days, for example, the interval between sowings may be longer. In a crossing block at Pakchong, Thailand (12° N), sowings were made at 12-day intervals: on Dec. 4, 16, and 28; yet there were differences of 4 to 8 days between days to 50% flowering. If these sowings were made in early March, the interval between flowering might well have been more than 12 days for some lines. When seed all from one parent is sown in one plot, sowing should be made at sufficient intervals to make all required crosses. For example, in the December sowings mentioned above, three sowings were made at 12-day intervals. In an early March sowing, however, five intervals would be used, with an increasing number of days between intervals: 0, 5, 8, 10, 12 days. It is expected that photosensitive varieties will flower quite late, hence early-flowering photoinsensitive varieties must be sown quite late.

Choice of Field

At the time of flowering, it is necessary to be constantly on the move—to be in the field all day every day—thus a compact field arrangement will prove most efficient (i.e., a square is more convenient than a long narrow rectangle). Because irrigation is often required for the fields during the flowering period when workers must be in the field, a well-drained nonsticky soil is advantageous.

Sowing Rate

Every effort should be made to grow plants with large heads. High fertilizer rates should be applied (150 kg/ha of N, with adequate amounts of other nutrients). Seed parent plants should be widely spaced: 75 to 100 cm between rows and 30 cm between plants. Larger heads will be obtained on widely spaced plants. The more seed obtained per cross, the fewer crosses must be made, or more different kinds of crosses can be made per season. A lot of handwork is involved in crossing; spacing the plants widely facilitates these operations.

Crossing Without the Use of Male-Sterility

Crossing to make F_1s for the purpose of selecting new varieties, or backcrossing to transfer a character, usually is done without male-sterility; thus plants must be emasculated. Although a large quantity of seed usually is not required, it is advisable to cross two or three plants per cross combination until experience is gained.

The crossing block book could be arranged as in Table 4.15 (also see the section on pedigree nomenclature, p. 78). Note that days late are indicated (i.e., parents are planted at different dates, so that some plants of both parents to enter a cross will be in flower simultaneously).

Three cross-pollinations are required for each cross combination; it is unimportant whether the cross is made 13 x 16 or 16 x 13. The notation "on or x's" indicates that reciprocal crosses are acceptable.

This crossing block is written as if rows 11 to 15 were somehow different from rows 16 to 25, so that crossing within these groups is not wanted. Such a situation might arise if rows 11 to 15 were a source of the gene for high lysine, for example. Otherwise, there is no reason that the cross 16 x 19 or 15 x 11 could not be made; organization depends on the objective.

The only limit in crossing is a restriction in the kinds of parents entering the cross, i.e., kafirs are not crossed with kafirs, feteritas are not crossed with feteritas, etc.

Crosses are usually made between relatively uniform lines, although not necessarily so. The parents are selected because they are agronomically elite and sufficiently different phenotypically so that genetic variability will increase. Crosses between select local types and promising exotic lines are good examples of this kind of crossing. Crosses also might be made to introduce a new factor such as male-sterility or high lysine, but this type of cross will generally lead to a backcrossing program, rather than the selection of new lines.

The F_1 generation will be uniform if the parents are uniform; segregation is first expressed in the F_2. A 2- to 5-m nursery row is sufficient to advance F_1 to F_2; however, the F_2 population should have at least 300 plants. If the F_2 population is restricted (say to a 5-m row) there are insufficient plants to observe the array of variation in the population. If there are many F_2 populations to be grown, it may be easier to use a 50-m row, than 10 rows 5-m long. No alleyways are required in the 50-m row, thus saving space.

Individual plants are selected in the F_2 to advance to the F_3. No selections may be made in some F_2 populations (discard), while many may be made in others. The breeder must use his best judgment, but there is no need to routinely save a few plants fom each F_2. It is suggested that at least 100 F_3 plants be grown, because there is still a large amount of variation. The population size can be reduced to 30 to 50 plants in subsequent generations. Yield evaluation can begin in the F_4 to F_5—it is more efficient to begin

Table 4.15: Format for crossing block field book.

Pedigree NES	Origin 72TA	Plot no.	Days to 50% fl.	Kind	Days late	Pollinating instructions
301	12	11	62	Kafir	1, 2 wk*	See rows 16-25
305	15	12	64	Kafir	1, 2 wk	See rows 16-25
438	23	13	59	Fet.*	1, 3 wk	See rows 16-25
445	26	14	73	Fet.	1 wk	See rows 16-25
553	40	15	75	Shallu	1 wk	See rows 16-25
101	601	16	80	Kafir		on or x's 13(3) 14(3) 15(3)
432	640	17	55	Kafir	2, 4 wk	on or x's 13(3) 14(3) 15(3)
436	642	18	62	Kafir	2, 3 wk	on or x's 13(3) 14(3) 15(3)
1209	803	19	65	Fet.	1 wk	on or x's 11(3) 12(3) 15(3)
1354	859	20	73	Fet.		on or x's 11(3) 12(3) 15(3)
1386	864	21	69	Fet.	1 wk	on or x's 11(3) 12(3) 15(3)
1401	901	22	62	Shallu	2, 3 wk	on or x's 11(3) 12(3) 13(3) 14(3)
1405	903	23	60	Durra	2, 3 wk	on or x's 11(3) 12(3) 13(3) 14(3) 15(3)
1406	904	24	80	Durra		on or x's 11(3) 12(3) 13(3) 14(3) 15(3)
1525	1033	25	65	Durra	1, 2 wk	on or x's 11(3) 12(3) 13(3) 14(3) 15(3)

* Fet. = Feterita, wk = week.

testing early, even though the yield trial plots may not be as uniform as desired.

Since selection in the F_2 (and possibly the F_3) populations is based on single plant selection in a variable population, plants should be grown with greater than normal spacing (25 to 30 cm between plants in the row) to allow for better individual plant expression.

Emasculation by Hand

If the crossing program is large (500 crosses or more), a crew is required to emasculate and another to pollinate and to keep the pollinating record current. A person with reasonable experience can emasculate 10 to 25 heads a day. (It takes a worker about 1 week to gain skill in emasculation). With a 10-man crew doing emasculation, a team of three workers is recommended for making the pollinations and keeping records. Such crews should be trained in advance of a large-scale crossing program. The same crew(s) should be available for several seasons, so that retraining is not required each season.

Equipment Required

The tools for hand emasculation are not complex, but good quality is worth the expense (Plates 7-6, 7-7, and 7-8). A strong manicuring plier with a spring to hold the handles open is convenient for trimming heads and works reasonably well for all trimming required. Small scissors are also useful for cutting away some florets in a cluster and for cutting away the pediceled spikelets if there is a possibility that they will shed pollen.

The tool used for removing the anthers can be made of an ordinary lead pencil or of wood (Plates 7-7 and 8-7); or it can be made quite easily by inserting a nail into a round stick and then filing the nail to shape (Plate 7-8). A sewing needle also can

be filed flat as shown on the right in Plate 7-8, but it is a bit too narrow. The general shape can be seen in the photograph—a flat, blunt end is needed, with the flat portion about 3- to 4-mm long, about ¼-mm thick, and about ¾-mm wide. The thinner the blade, the better; but it should not be sharp. The point should be polished with very fine sandpaper or an emery stone; if there are rough marks on the blade, the anther filaments will catch, making it difficult to remove them from the tool. Some workers prefer a fine-pointed tweezer for emasculation—the spring action of the tweezer opens the floret and the two tips of the tweezer are used to remove the anthers.

The earshoot caps or glassine bags used by maize breeders are convenient for covering the head following emasculation. Plastic should not be used, as it is water-tight and moisture from transpiration results in an undesirable wet microclimate in the bag. Paper clips are required for clipping the bag to the head—staples should not be used as the bag must be removed to inspect the head to see if it is ready to pollinate, and for the pollination operation. A small jar of alcohol is convenient for cleaning the emasculation tool in case an anther is ruptured and pollen adheres to the tool. The pollen is killed by dipping the tool into the alcohol. A small square-topped (about 25 cm) table is useful for holding the working items for the field worker. A small stool will make work more comfortable. These stools should be adjustable in height, or several heights should be available. The sorghum head will vary in height from 70 to 400 cm above the ground.

The Floral Structure

The pediceled spikelet is long and narrow, usually devoid of floral parts. There are one or two pediceled spikelets for each sessile spikelet. The floret contains the floral parts: one ovule from which two pistils protrude, each tipped with a fluffy stigma. The stigma varies in length from ½ mm to 1 ½ mm; it is usually white, but may be yellow or pink. The stigma is attached to the ovule by a reasonably strong style (Plate 8-4). Three anthers are attached at the base of the ovule by a very fine filament; these anthers must be removed by emasculation. The floret is encased by two glumes; during emasculation, care should be taken that the glume closest to the pediceled spikelet be held facing away from the worker. While trimming the head, it is advisable to trim all florets so that they face the same direction, i.e., most florets will face toward the outside of the head. Those at an angle to these florets should be trimmed away, as they are more difficult to emasculate and usually are damaged so badly in the process that they do not set seed. (Plates 7 and 8).

The Emasculation Operation

The trimming of the head for emasculation requires about as much time as does removing the anthers (Plates 7 and 8). Preferably, the head should begin to flower before emasculation. Three to five days are required for flowering over the whole head; flowering begins at the tip of the head and proceeds to the base. Generally, the best section to emasculate is that part of the head that would be ready to flower on the next day. In some instances, a gap of 2 days is better. A satisfactory technique is for one or two people (pollinating crew) to trim the heads, while field labor does the emasculations. This procedure provides for a better selection of panicle branches for emasculation. If emasculation is done on florets that would normally flower 3 to 5 days afterward, they are usually damaged so badly that there will be little or no flowering. If emasculation is done on florets more than 5 days before they would normally flower, flowering will not occur and the head is lost. Generally, 25 to 50 florets should be left on three or four panicle branches. It is advisable to trim away florets close to the rachis as it is difficult to grasp them with the fingers. Trimming may be done so that individual florets remain uniformly spaced along the panicle branch, or done so that the florets occur in clusters of two or three. If more florets should remain, the chance is increased that one will be missed during the emasculation operation. These anthers, if undetected, would later shed pollen and cause self-fertilization.

Emasculation is done by grasping the floret between the thumb and forefinger (Plate 8); the pediceled spikelet is held away from the operator. The emasculation needle is turned so that the flat portion is parallel to the opening between the glumes. The needle is inserted just below the middle of the floret, then moved toward the back glume, and across the floret. The needle is then rotated slightly and lifted—the anthers come up and can be removed. If an anther breaks, the fragments should be removed along with the ovule that may have been self-pollinated.

Varieties differ in ease of emasculation. The small, stiff-glumed types are the most difficult, and the effort may not be worthwhile. These types should be used as pollinators, if possible. The larger and softer-glumed types are easiest to emasculate. Occasionally, the pistils come up readily with the anthers; if this occurs, the pistils can be pushed

Text continues on p. 102

PLATE 7. CROSSING IN SORGHUM - 1

7-1 The male-sterile head just beginning to flower; while backcrossing to develop new seed parents, the head is observed at this stage to see if it is completely sterile. Pollination is made only on fully male-sterile plants.

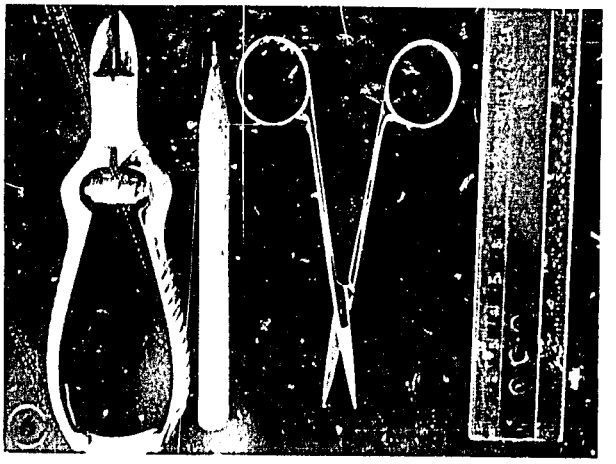
7-2 Cutting away the flowered tip prior to bagging. Having flowered, the tip florets would be randomly crossed, so they must be cut away to avoid contamination.

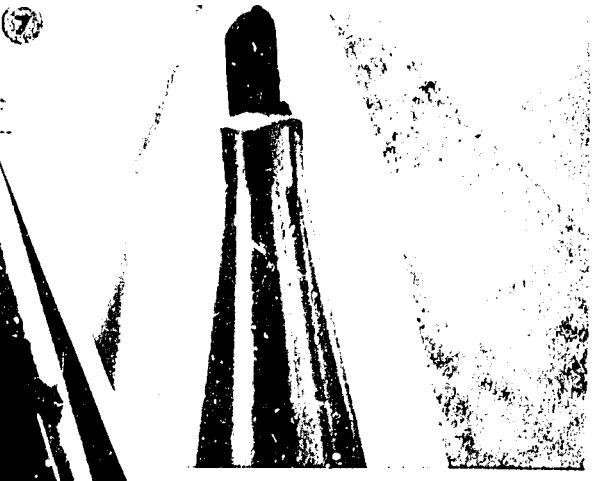
7-3 A head that is at a good stage for hand emasculation.

7-4 Cutting away the flowered portion of the head.

7-5 The lower panicle branches have been removed, leaving selected branches (those that would normally flower the following day; i.e., just below the flowered portion). The number of florets is being reduced to about 50 by trimming so that florets remain in clusters of two or three.

7-6,7-7,7-8 Equipment useful for emasculation. The manicuring clipper is useful to trim the head, while the surgical scissor is useful for trimming the panicle branch and cutting away the pediceled spikelets. The emasculating needle, made of wood (7), or a filed nail mounted in wood (6 and 8), is flat and thin (the size is compared to fine-sized lead in a mechanical pencil in 7 and 8). It is necessary that the needle be very smooth so that anthers will not cling to it—an irritating occurrence while emasculating. The filed needle shown at the right in photograph 8 is too narrow.





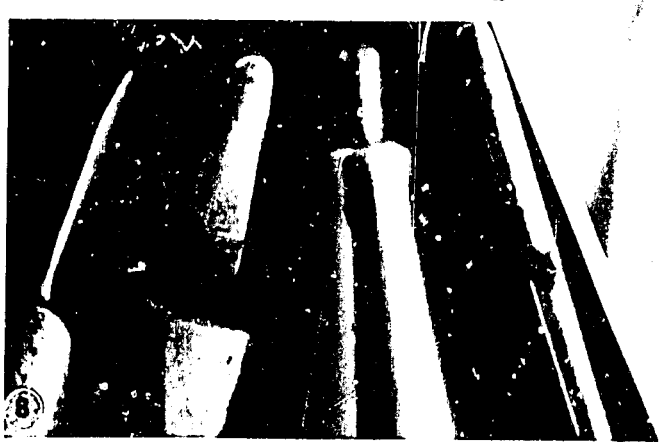


PLATE 8. CROSSING IN SORGHUM - 2

8-1 Trimming away the pedicelled spikelets; this must be done only if fertile anthers develop in these spikelets.

8-2 Position of hands while emasculating.

8-3 The head fully trimmed and ready for emasculation.

8-4 The sexual structures showing ovule, two styles with attached stigmas, and three filaments with attached anthers.

8-5 The emasculation needle is inserted at the middle of the floret and moved across the glume behind the anthers.

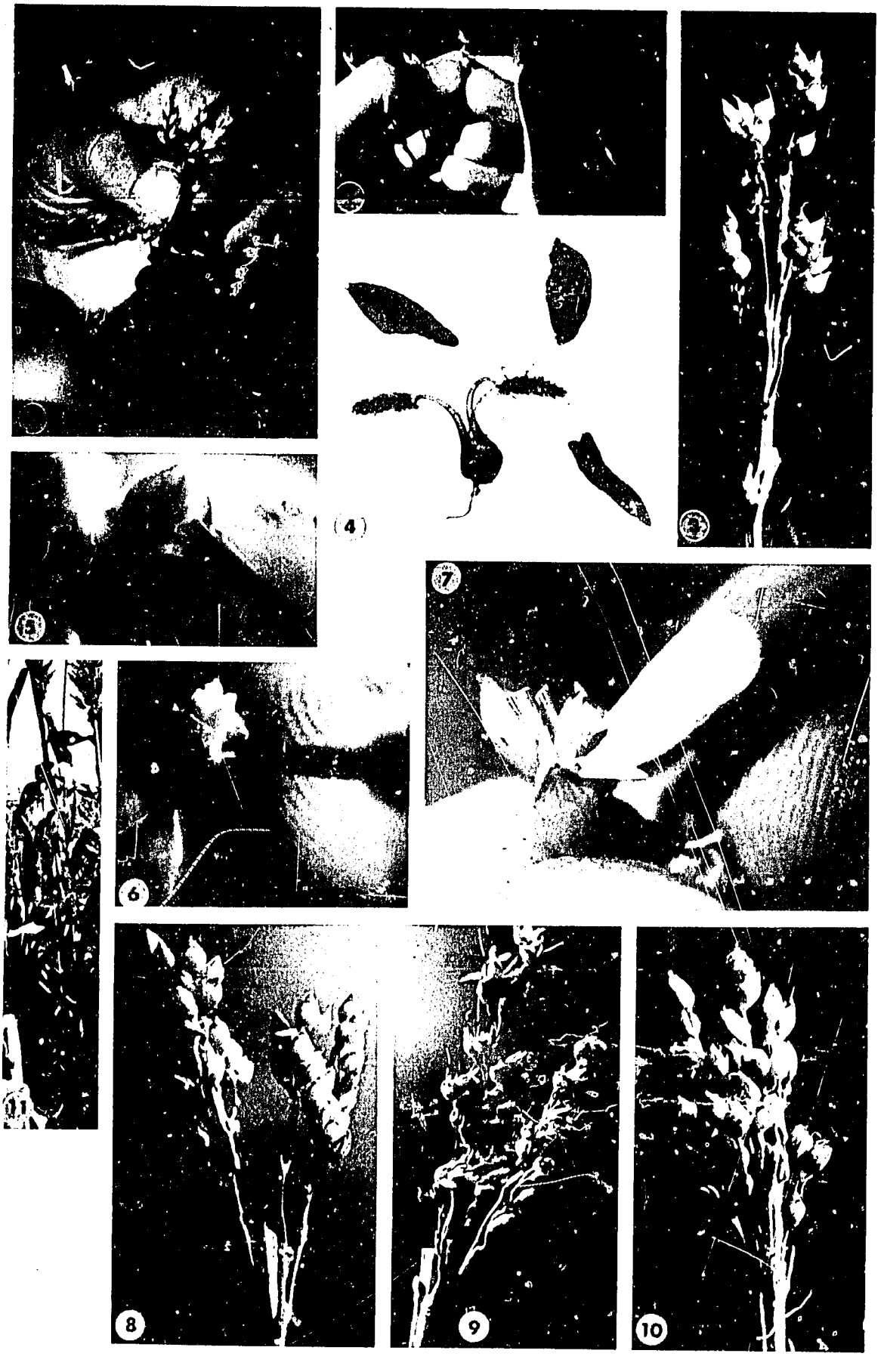
8-6,8-7 The needle is rotated 90° and the anthers lifted out.

8-8 Florets containing missed anthers frequently flower a day or two before the others. Daily inspection of the emasculated heads (translucent glassine maize ear shoot bags are useful) is worthwhile both to organize the pollinating program for the following day and to remove such anthers.

8-9 An emasculated head in full flower and ready for pollination. Frequently 2 days are required for the head to flower fully.

8-10 Seed developing after pollination. Seed set varies between 10 and 80%, depending to a considerable extent on the operator's skill; however, plants with small stiff glumes are very difficult to work with and should be used as pollen parents.

8-11 Self-pollinated seed parents showing up in seed harvested from a cross-pollinated head (after head emasculation). Seed parents should always be sown with the F_1 plants so they can be identified and removed.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down into the floret immediately after the anthers are removed. (The other heads should be trimmed by selecting panicle branches further down the head, trimming so that flowering would normally be expected 2 days later.)

The pollinating crew should check each day for heads that have flowered sufficiently for pollination the next day. The date of emasculation should be marked on each bag at the time of emasculation (Plate 9). Heads that are likely to be ready for pollination can be identified by this notation. Frequently, 2 or 3 days are required for complete flowering of the emasculated head. Florets having one or more anthers that have not been removed will frequently flower a day before the properly emasculated ones. Such florets can be trimmed off at this inspection, thus avoiding much self-pollination of emasculated florets. When it is decided that a head should be pollinated the following day, a paper clip or mark should be placed on the bag covering the head. This will help to locate the head quickly during the busy period of pollination on the following day.

Emasculating with the Hot Water and Plastic Bag Technique

Note: The author prefers emasculating by hand, using a needle or tweezer, because all seeds obtained are F_1s. Usually the problem is not in making crosses, but in evaluating the F_2 populations.

A bag made of a plastic sleeve is tied closely around the peduncle to surround the sorghum head. The bag is raised and lowered by a pulley suspended from a tripod. Very hot water is brought to 42° C by mixing with cold water in a bucket; it is then poured into the closed plastic sleeve. The head is soaked for about 10 minutes. The percentage of sterilized florets varies, but some self-pollination usually occurs, and selfed plants must be identified in the F_1 populations (Stephens and Quinby 1933).

The plastic bag technique is effective because the high humidity created in the plastic bag prevents dehiscence. The floret opens and the anthers emerge but shed no pollen (these anthers can be knocked free of the head by tapping). Abundant pollen from a dry head is used for pollination. The plastic bag (in a paper bag) is placed on the head about 4 p.m.—after the heat of the day. Pollination is done as soon as the paper and plastic bags are removed. The head can be pollinated repeatedly, or the nonflowering panicle branches can be removed. The paper bag only can be placed back over the head with a notation indicating the cross made. The F_1 seed obtained generally ranges from 40 to 90% (Schertz and Clark 1967).

Pollination

Pollination should be made as soon as all, or almost all, of the florets come to flower. All florets might not flower. If some florets scattered over the head are ready, then the pollination should be made the next day—further delay usually will not result in more florets coming to flower. The receptivity of the stigma is best just after it emerges from the floret and remains good for several days. Afterwards receptivity declines, and after 10 days receptivity is only about 1/30th of that of the first day.

Pollen usually sheds just before or shortly after sunrise on dry mornings, of if there is much dew, shortly after the head dries. Heads emasculated at this time are more likely to be contaminated than those emasculated later in the morning or in the afternoon. If pressure of work allows, emasculation should be done only in the afternoon. The pistil comes up with the anthers in a few varieties, and these rows could be emasculated in the afternoon (working on other varieties in the morning hours).

Tillers can be used for both emasculation and pollination although they may be much smaller than the main stem (they are frequently slighter in stature and taller than the main stem), they are identical genetically.

Pollination should begin soon after normal pollen shedding is over in the morning. Pollinations made when the air is full of pollen are more likely to be contaminated than pollinations made later. On a dry morning, when normal pollen shedding is occurring between 6 and 7 a.m., the hand pollinations might begin around 9:30 or 10 a.m. If normal pollen shedding is delayed until 9:30 or 10 a.m. because of rain or dew at night, the hand pollinations might be started at 11:30 or 12:30 in the morning. Delaying pollinations into afternoon hours probably should be tested as a technique to be sure that good seed set is obtained.

Sorghum pollen kept in a pollinating bag does not live long—10 to 20 minutes is about maximum time for holding. Some varieties store better than others—pollen of some varieties forms clumps soon after the pollen is shaken from the heads into the bags. Old pollen may clump, forming particles that are bigger than the pollen grain itself; its color may be orange. Good pollen is usually a lemon yellow; however, pollen of many varieties remains lemon yellow even when very old. For varieties in which the

pollen readily clumps, pollinations should be made within a minute or two after collection. Clumping of pollen increases when the humidity is high.

Pollen in the anthers remains alive several hours after normal pollen shedding. Heads protected from wind will hold most of the pollen; this pollen may then be liberated when needed by tapping the head vigorously with a finger.

There are several techniques for collecting pollen; local conditions will determine which to use. For example, appropriate heads may be bagged on the night before the pollen is needed. This technique is useful if the nights are dry and there are strong early morning breezes. Or heads can be inserted into bags in the morning and pollen shaken from them. This technique is useful if there is heavy dew at night and very little air movement during the morning hours. Another technique is to clip the heads from the plants early in the morning, before pollen shedding, and place them in boxes or flower pots kept in a protected place. This technique is effective if the dew is heavy at night and there are early morning winds; it is also useful if the head is a poor pollen shedder. Some heads of sorghum shed quite a bit of pollen (one quarter of teaspoonful), but many shed very little. If a paper bag is used, much of the pollen may adhere to the bag; wiping the pollinator head on the seed parent head is a better technique under most circumstances (Plate 9-6).

The first and last days of flowering are poor times to use a head for pollination, as more pollen is available during the days in the middle of the period. The same head may be used several times as a pollinator and then emasculated and used as the seed parent if only the flowering portion of the head is cut each day.

Contamination from foreign pollen on heads used as pollinators has never been found to be great enough for concern. The best technique for maximizing seed set should be developed; stray pollen will probably not be a serious contamination problem. If better pollen is obtained by cutting heads or collecting pollen in bags in the morning, then this method should be used—rather than bagging the heads on the previous night to protect a pollinator head from stray pollen that might subsequently cause an unwanted cross-pollination.

When pollen is collected from a head that has been bagged the previous day, the bag should be pulled downward as it is slipped from the head (Plates 9-1 and 9-2). Usually the plant can be bent to the side to help this operation. If the bag is not pulled downward, much pollen can be lost.

If there is doubt about the quantity of pollen in the bag, a visual check can be made (Plate 9-3). Even small amounts of pollen can be seen in the bag if the sunlight is directed properly. Pollen should be seen (rather than anthers; the fact that anthers are found does not ensure that there is pollen). If a slight yellow dusting of pollen is seen inside the bag, a sufficient amount is probably available. At times, a cloud of pollen can be seen if the bag is tapped with the finger. Glassine bags are good for collecting—because the paper is slick there is less chance for the pollen to adhere to it. To avoid contamination while manipulating the bag, either for pollinating or inspection, the fingers should not be placed in or around the opening of the bag. Techniques can be developed so that fingers do not come into contact with the bag opening (Plates 10 and 11).

Field Records

A field book is required to keep track of the crossing operations. It should indicate all crosses to be made in each plot, and there should be sufficient space for notes such as days to 50% flower, and for any special comments. A continuous record should be made of the number of pollinations made each day. This can be done on the row tags (if the number of combinations are few), or in the field book (Plate 12).

Workers responsible for a crossing program must be sure that the proper number of cross-pollinations is made of each combination required. If the number of combinations is large, these workers should check the availability of heads per plot ready for pollination, as well as heads available to be used as pollinators. A record of completed crosses must be kept. (Over 500 different combinations were made at Farm Suwan near Packchong, Thailand, in one month; the technique used for keeping track of pollination is outlined in Plate 12-1 to 3 as an example of a procedure that has worked satisfactorily).

Plate 12-1 shows a daily record sheet: the numbers 1 to 50 are plot numbers, and the fractions under the column head "o/o" indicate the number of heads shedding pollen/number of heads ready to receive pollen (emasculated heads) on the following day.

Plate 12-2 shows the layout of a diallel crossing program that served as a continuous record of crosses made, i.e., each day's crossing would be indicated on this sheet until the desired number were complete. Plate 12-3 shows how such a sheet is used to determine the required number of

Text continues on p. 112

PLATE 9. POLLINATION

9-1, 9-2 Removing the pollinating bag from the head. After the pollen has been tapped from the head, the head must be bent as far to the side as possible without breaking the stem, and the bag rotated downward while removing it. If this process is not followed, pollen will spill and be lost.

9-3 Checking the bag for pollen. Some plants shed little pollen, and one must direct the sunlight properly into the bag to see it. Normally, however, the lemon yellow pollen can be easily seen collected in the bottom of the bag. The presence of anthers (foreground of photograph) does not indicate the presence of viable pollen; good pollen can be seen in the background of the photograph.

9-4 Marking pollinating bags for special techniques. Different colors can be rapidly painted onto bags by slipping the bundle of bags sideways and painting the exposed edge.

9-5 The pollinating apron. Pockets are make to hold pollinating bags, marking pencil, clips and/or stapler, knife, and field book. Such an apron is a convenience to field operations.

9-6 A pollinating technique. This technique is better than the one shown in photographs 1 and 2; considerably more seed is obtained per cross. The head is cut from the pollinator plant early in the morning and used for crossing after flowering takes place (flowering readily occurs in a head cut earlier the same morning).

9-7, 9-8 The problem of fading ink. Some ink and pencil markings fade in the weather—only nonfading ink and pencils should be used. Both photographs were taken on 16/2, showing that one ink (marked on 4/2) was still dark, while a second marked 5 days later (9/2) had already begun to fade (the ink used to mark the 9/2 was also used to mark the 16/2).

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13X21

3

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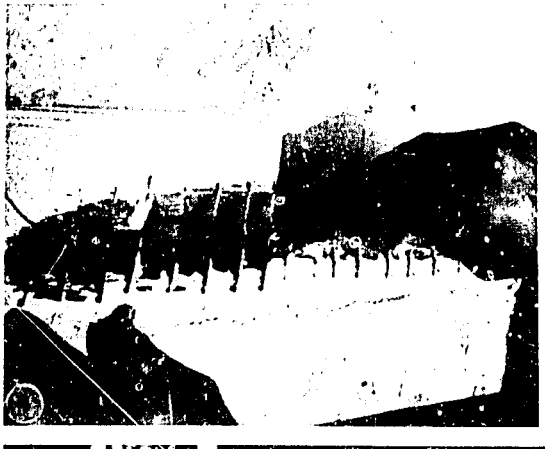

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PLATE 10. MANIPULATING THE POLLINATING BAG

10-1 Holding the bag in preparation for making a pollination. The objective is to place the bag over the head without loss of pollen and without placing the fingers around the bag opening (which would lead to contamination). The bag is held with seam away from the operator, the bag being grasped between the thumbs and second fingers (thumb in front, second finger in back). The first fingers are placed into the folds of the bag.

10-2 The first fingers are moved forward over the thumbs pulling the open end of the bag forward until it is approximately at a right angle to the bottom of the bag.

10-3 The hands are rolled together until the knuckles touch, thereby crimping the bag together.

10-4 The bag is grasped by one hand and placed over the head.

10-5 The bottom of the bag is clasped around the peduncle with one hand, pulled straight with the other, and pumped vigorously up and down, filling the air within the bag with pollen.

10-6,10-7 A second technique, where the bag is first folded (which is normally done just after the pollen is collected and prior to carrying it to the seed parent): The inside folds of the bag are held between the thumb and first finger, and the second finger pushes the bag open. The bag is placed over the head, and the same process as shown in photograph 5 is carried out.

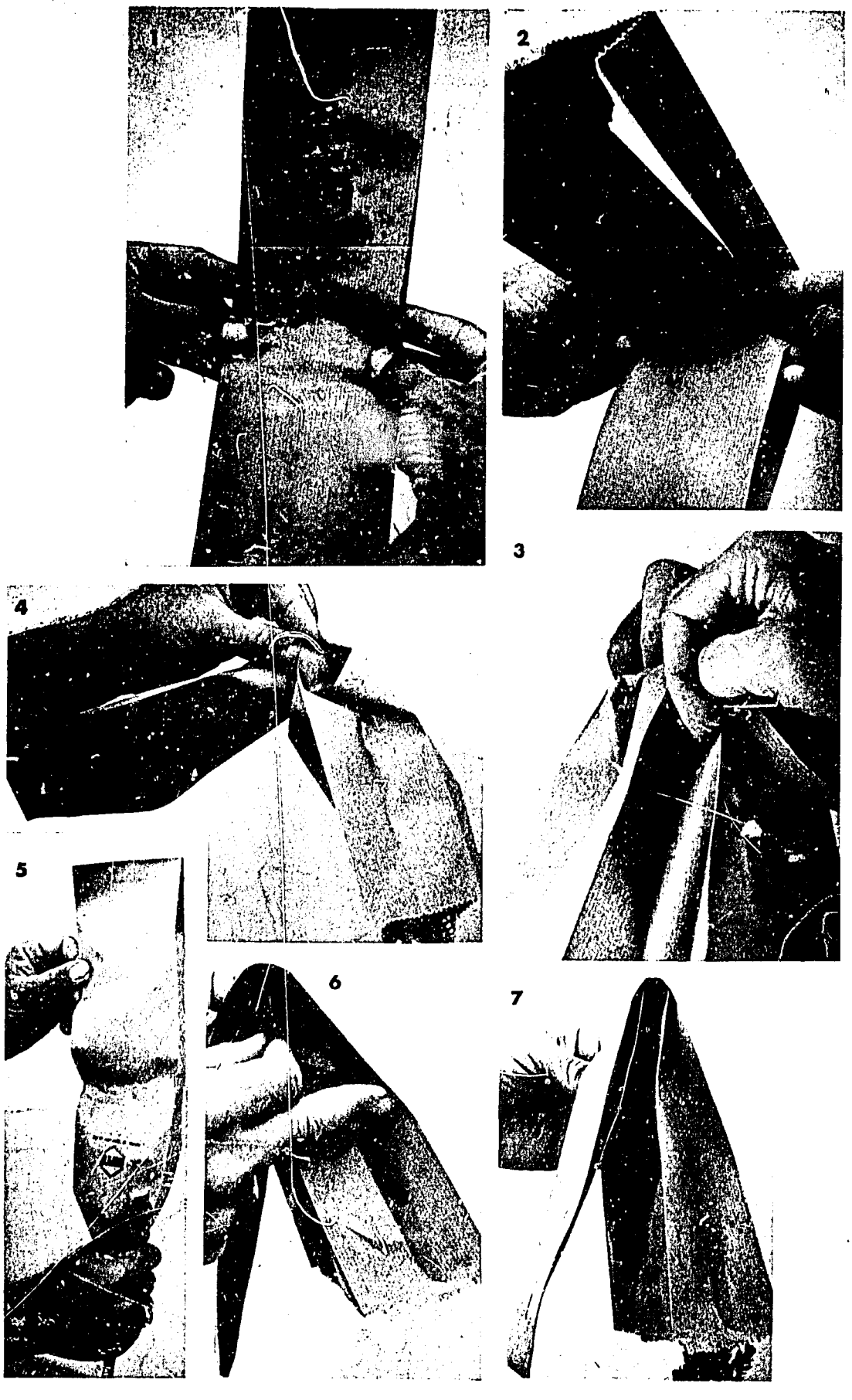
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PLATE 11. CLOSING THE POLLINATING BAG

11-1 After a pollination is completed, the bag is secured over the head. The bottom corners are grasped between thumb and fingers and folded in by sliding the finger across the thumb and rotating the hands in, or by placing the first fingers along where the folds will be and pushing the corners up with the thumbs.

11-2 The folded corners are brought together.

11-3 A staple or paper clip is placed to hold the corners together. The staple or clip should be placed so that the bag will not blow off the head but not be so tight that the head will push through the top of the bag rather than for the bag to move as the head and peduncle elongate. Clipping a leaf into the fold is not usually desirable. A paper clip should be used if it will be necessary to open the bag several times before harvest.

11-4 A second way of folding the corners of the bag together.

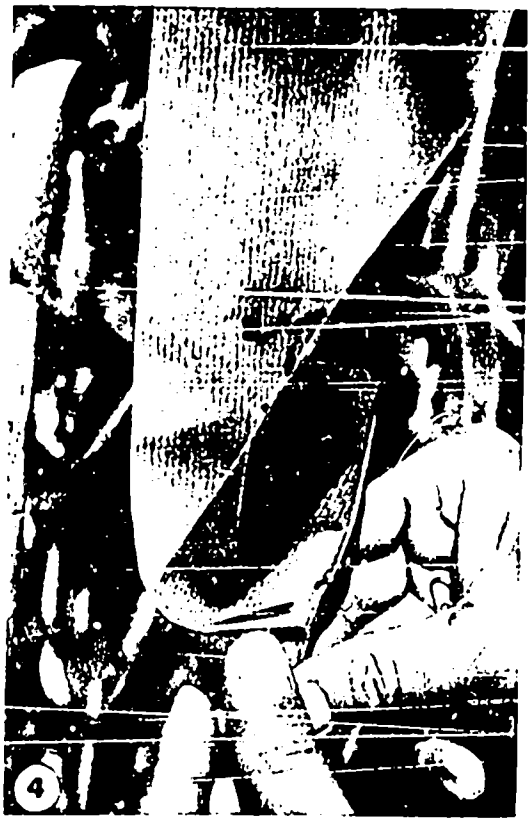


PLATE 12. FIELD RECORDS FOR HAND CROSSING

12-1 Daily work sheet on which numbers of heads in flower for each plot are indicated. From this work sheet the crossing program was developed for the following day (see text for details).

12-2,12-3 Master sheets used to indicate crosses desired. During the pollinating season such sheets are useful to indicate numbers of crosses made and the number required for each combination (see text for details).

ROW TAGS

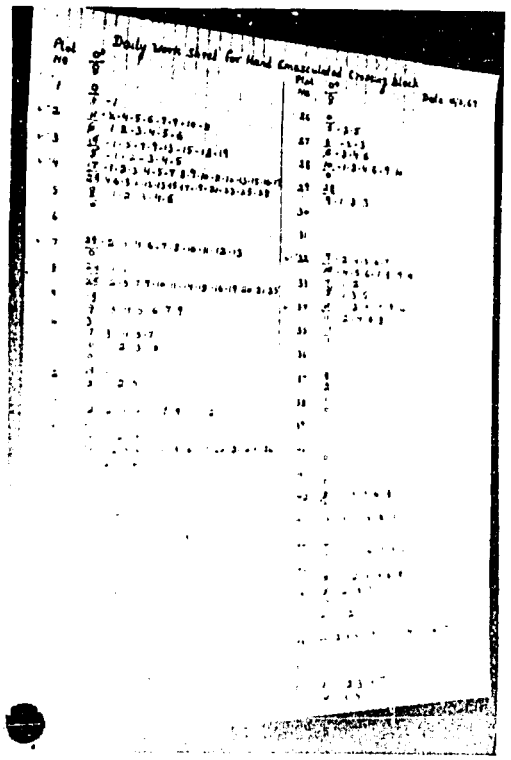
12-4 The row tag should be a field convenience: one should be placed on every row, and plot numbers should be on both sides of the tag. Hunting for row tags takes time; make them conspicuous (yellow is a good color to use) and of reasonable size; place them where they can readily be seen. Pollinating instructions can also be marked on row tags.

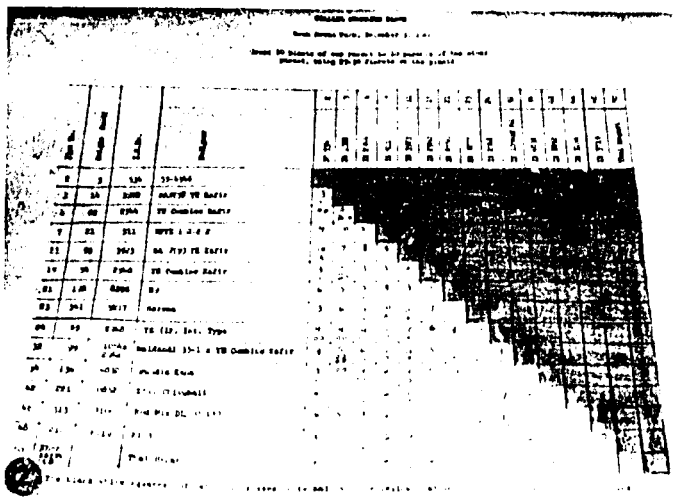
12-5 Plot numbers should be marked on the top and the bottom of row tags. At harvest, the bottom portion of the tag goes into the harvest bag and the top portion is used to close the bag.

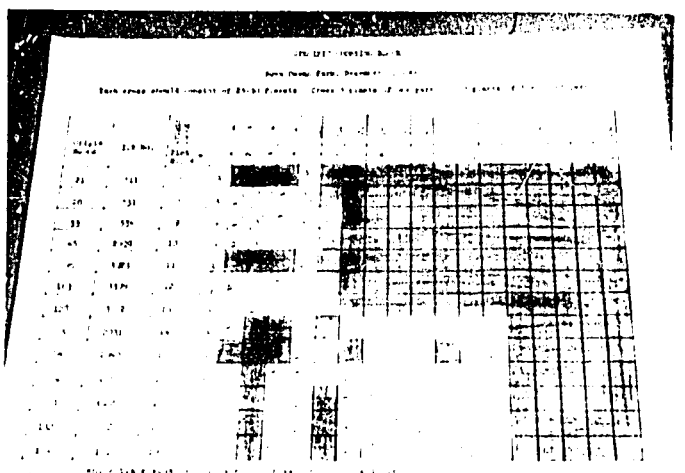
12-6,12-7 Loss of row tags, especially in stormy weather, can be reduced if the tag does not pull away from the retaining wire—reinforcement of the hole in the tag is important.

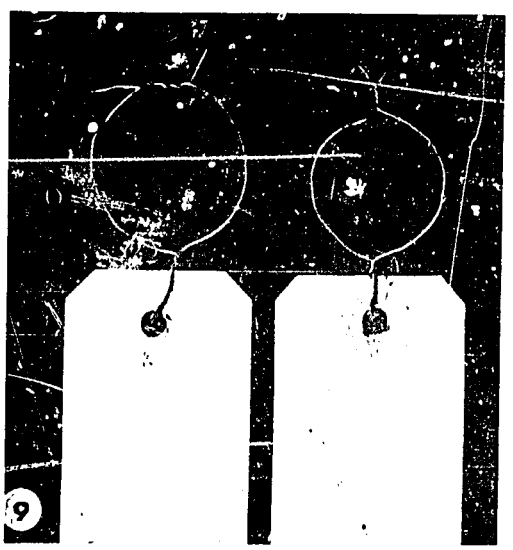
12-8 The row tag can be folded and clipped when all desired pollinations have been made. This is a signal that the row is complete, thus saving time for the pollinating crew.

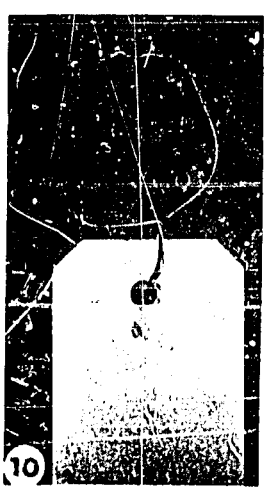
12-9,12-10 A simple loop is sufficient to hold the tag on the plant. The loop should not be tight or it will squeeze the plant during later growth. If the wires are fastened as shown on the left-hand side of photograph 9, they can be separated by simply jerking them apart (photograph 10), rather than unwinding as would be required for the tag shown on the right-hand side of photograph 9. If the plant is to be fed to animals following harvest, string, rather than wire, should be used to fasten tags to plants.

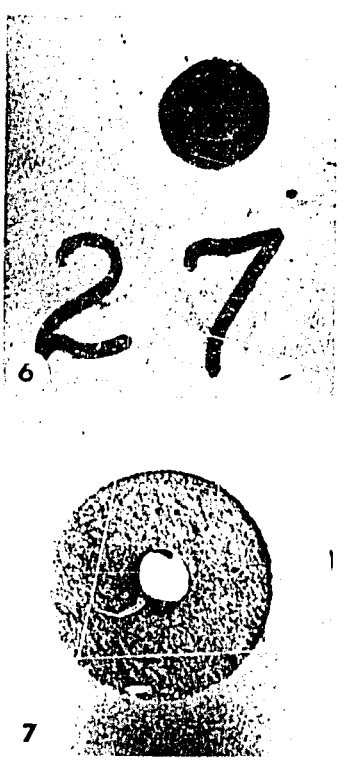

Daily work sheet for Hand Crosscutting Cherry block







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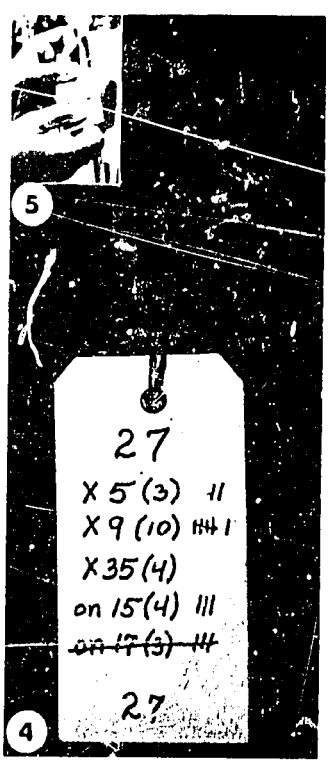

27
X 5 (3) II
X 9 (10) IIII I
X 35 (4)
on 15 (4) III
~~on 17 (3) III~~
27

crosses. In this case, three cross-pollinations were required per combination. The detail for plot 18 (horizontal row) is shown in Table 4.16.

The daily worksheet for plot 18 reveals the following notation (Plate 12-1):

$$\frac{1}{8}\ \begin{matrix} -1 \\ -1\ -2\ -3\ -4\ -5\ -6\ -7\ -8 \end{matrix}$$

The -1 next to the numerator of the fraction was written when row 18 was assigned as pollinator (the cross 18 x 10). The -1 was written next to the denominator when the cross 18 x 2 was established; -2 was written when the cross 18 x 4 was indicated; -3 when 18 x 5 was indicated, etc. When the number of crosses indicated reached -8, no more crosses involving plot 18 could be made. This same process was repeated for every plot. Using the master sheet (Plate 12-3), the pollinating bags could be properly labeled (i.e., 18 x 2 would indicate that row 18 was seed parent, row 2 the pollen parent). The cross 18 x 10 would actually be written 10 x 18 on the pollinating bag because row 18 is the pollen parent. After all pollination bags had been marked, they were taken to the field and placed on the desired plants (into row 2 for the 18 x 2 cross and into row 18 for the 10 x 18 cross). After the crosses were completed on the following day, the 0's and ✓'s were removed from the master sheet, and the number 2 in the cross 18 x 2 was changed to a 3.

Although fairly complex, this system of field recording accounted for over 500 combinations, requiring some 3000 head emasculations (note on Plate 6, page 92). Without such a method for determining the daily requirement for crosses to be made, it is likely that many required crosses would not have been made, and perhaps too many crosses of other combinations would have been made. If the number of plots involved is smaller, or if there are few combinations between any two plots, then daily records can more easily be kept on row tags (Plate 12-4; a discussion of this technique is presented on page 149).

Often a checkerboard can be made for recording purposes, with female parents listed down the left side and male parents across the top. Each time a cross is made, a check can be placed in the appropriate square on the checkerboard.

Crossing Block for Making Hybrid Seeds on Male-Sterile Female Parents

A, B, and R Lines

Hybrid sorghums are produced with crossing a male-sterile seed parent (Plate 6-3) with a male-fertile pollinator parent. The male-sterile seed parent is produced by crossing the male-sterile plants with pollen from a pollinator parent called a *maintainer* . The male-sterile seed parent is called the *A-line*, and its maintainer is called the *B-line*. When the A-line is crossed by its B-line, the seeds produced will result in A-line plants; i.e., the B-line is nonrestoring on the A-line. The A and B lines are isogenic (phenotypically the same), except that the A-line is male-sterile and B-line is male-fertile.

A-line x B-line--------→ A-line

Hybrid seed is produced by crossing the A-line by an *R-line* (restorer line). Plants grown from the

Table 4.16: Daily records for a crossing program.

	Cross combination	Operation
Plot	18 x 1	Completed
	18 x 2	2 crosses finished, the '0' indicates that one more cross pollination is required using plot 18 as seed parent.
	18 x 3	Combination not wanted
	18 x 4	Same as for 18 x 2
	18 x 5	Same as for 18 x 2
	18 x 6	Combination not wanted
	18 x 7	Completed
	18 x 8	Completed
	18 x 9	Completed
	18 x 10	Same as 18 x 2 except that row 10 is the seed parent and row 18 the pollinator parent (indicated by the ✓).

seeds produced by this cross are male-fertile; i.e., the R-line is restoring on the A-line. The R-line is not phenotypically similar to the A-line; it is selected so that the cross will result in a high-yielding hybrid.

A-line x R-line-------→ male-fertile hybrid

Obtaining Adequate Quantities of Hybrid Seed

A hybrid program requires that a large number of crosses be made for yield evaluation. Preliminary yield testing will require many hybrids. Seed for the fewer hybrids going into a countrywide regional test might well be made in open-pollinated, isolated fields. The crossing operation can be done in an off-season for stations that can grow only one crop a year. An off-season location in a more tropical region may be required for stations that have cold winters. Crossing in support of regional yield trials must be done on a large scale if it is to be effective. For example, 15000 cross-pollinations were made one year and 20000 the next year at one southern location in India—to provide hybrid seed for regional trials and for several northern stations. Efficient organization of field personnel is required to accomplish this amount of work.

Organizing Decisions

A number of initial decisions must be made in organizing a crossing block: how much seed is required of each F_1; how much seed will be obtained per cross; what is the range of flowering dates among entries in the crossing block (and, knowing this, how many dates of sowing are required for each entry); how many days' interval should there be between sowing dates; and what are the relationships among entries? The following examples will demonstrate how such decisions can be made.

Seed Required: Suppose that a hybrid trial is being planned for three locations. Each trial will have four replications, with 4-row plots 5-m long, and with 15-cm spacing between plants. There are three locations x 4 reps x 4 rows = 48 rows total. With plants 15-cm apart in a 500-cm row, there are 500/15 = 34 hills (plants) per row, or 34 x 48 = 1632 hills total. To determine the amount of seed required, it can be figured that the weight of sorghum seed is about 2.5 g per 100 seeds. Thus 1632/100 x 2.5 g = 40.8 g of seed is needed if germination is 100% and one plant per hill is required. Germination is never 100%; if the germination percent is not known, it is usually safe to assume 50%. Therefore about 82 g of seeds are needed. This is a minimum amount of seed and would require spaced sowing. If the seed is to be sown by drilling, a total of 120 to 150 g is recommended. About 30 to 40 g of seed per cross can be obtained on a cytoplasmic sterile head, but it is better to estimate 20 g. Thus, to obtain a total of 120 g of seed, the cross-pollinations should be 120/20 = 6.

Calculating Sowing Dates: It is generally best that all pollinators be sown in one block and all seed parents be sown in another. This requires that the seed parents are sown in blocks on different dates. The dates of sowing will vary and must be determined by local information and experience. In the tropics, many male-sterile seed parents flower in 60 to 70 days and the earliest pollinators will flower in 50 days. Hence, the first sowing of male-steriles should be made 10 days to 2 weeks before the pollinators are sown. Three additional sowing dates are useful: on the same date as the pollinator, 2 weeks later, and 4 weeks later. Parents that vary in flowering by more than 10 days usually should not be crossed to make hybrids for yield trial purposes; commercial seed producers would find it too risky to achieve a good nick in the production field. The off-season crossing block may be sown when days-to-flowering of photosensitive types is increasing, and this must be taken into account in estimating sowing dates. It is generally not advisable to continue a line (although it may be a good parent), if it is a poor pollen shedder, difficult to propagate, or for some other reason troublesome. The trouble will continue for the seed producer for the entire time the hybrid is in use.

The field book, including crossing instructions, is written as shown in Table 4.17.

Days-to-flowering are continuous, but entries should be grouped so that sowing dates will fall at 1-week intervals. This will avoid the necessity of too-frequent trips to the field to plant. Flowering will be sufficiently variable to provide pollen when required. To calculate days-late, plot 11 may be used as an example. It flowers in 62 days; the parents in the cross 11 x 19 differ in flowering by only 3 days; hence no stagger in sowing date is required. The parents in the cross 11 x 20 differ in flowering by 11 days. It is recommended that hybrids with parents differing by more than 10 days not be considered, because of seed production problem if such hybrids should ever be produced commercially, thus this cross would be dropped. The parents in the cross 11 x 21 differ in flowering by 7 days and row 11 is the early parent; therefore, row 11 is sown on the first date and 7 days later, so that it will nick with row

21. Days-late is determined for other seed parents in the same way. Note that in cross 15 x 21, the pollinator parent (21) is 6 days earlier than the seed parent; in this case, the pollinator parent is sown on the first date and then 1 week later.

Writing Instructions: Several factors must be considered while writing the pollinating instructions. First, the parents to be entered into a cross are represented by row number, i.e., 11 x 19 (not NES 501 x NES 1209). The pollinating instructions are field instructions, and the plot tags carry only row numbers. Pollinating instructions given in terms of plot numbers relate effectively to plot tags.

Secondly, no cross should be made if the days to 50% flowering of the two parents exceed 10 days, for the reason cited above.

A third consideration concerns relationship: a kafir would not be crossed with a kafir or a feterita with a feterita; hence the cross 11 x 18 would not be made.

As indicated earlier, six heads would be pollinated for each cross combination; therefore, the symbol "11 x 19(6)" indicates that six cross-pollinations of 11 x 19 are to be made. Adequate space should be left between pollinating instructions to accommodate "1" six times (i.e., 11 x 19(6) 1). A mark is entered each time a cross is made, thus providing a record of crosses finished and crossing yet to be done.

Pollen Collection: The procedure for collecting pollen will determine the quantity of seed obtained per cross. Because of weather conditions, it may not be possible to bag pollinator plants on the day before pollination (the bags might remain damp from dew until late in the morning). In these conditions it is questionable that bags should be used anyway, because frequently there would be poorer seed set than that obtained by other techniques. In Coimbatore (India) initial crosses were made by cutting heads, immediately carrying the heads from pollinator plant to seed parent, then wiping the pollinator head on the seed parent head. A single head was used until all pollen had been used. Seed sets ranged from 2 or 3 g to 20-30 g per head, but this was very poor, since a full head would produce 70 to 80 g of seed. Even less seed was obtained when pollen was collected in bags and shaken from the bag onto the appropriate heads. The procedure developed by Orrin Webster at the University of Nebraska, USA, was used with much greater success. Heads were cut from pollinator plants early in the morning (before dehiscence) and placed in a container. Pollen will not shed as long as the heads remain undisturbed in the container. These heads, full of pollen, can—even after several hours—be wiped across the seed parent head. (This technique is particularly valuable if there are early morning winds that blow the pollen from the heads, thus reducing the time available for making cross-pollinations.) Heads from one parent only were placed in each

Table 4.17: Field book format including crossing instructions.

Pedigree NES	Origin 72TA	Plot no.	Days to 50% fl.*	Kind	Days late	Pollinating instructions
501A	25	11	62	Kafir	1 wk	× 19(6) 21(6) 22(6) 23(6) 25(6)
505A	27	12	64	Kafir	1 wk	× 19(6) 20(6) 21(6) 22(6) 23(6) 25(6)
632A	29	13	59	Feterita	1 wk	× 17(6) 18(6) 22(6) 23(6) 25(6)
633A	31	14	73	Feterita	1 wk	× 16(6) 24(6) 25(6)
654A	35	15	75	Shallu	1 wk	× 16(6) 19(6) 20(6) 21(6) 24(6) 25(6)
101	601	16	80	Kafir		on 14, 15(6)
432	640	17	55	Kafir		on 13(6)
436	642	18	62	Kafir		on 13(6)
1209	803	19	65	Feterita	1 wk	on 11, 12, 15(6)
1354	859	20	73	Feterita		on 12, 15(6)
1368	864	21	69	Feterita	1 wk	on 11, 12, 15(6)
1401	901	22	62	Shallu		on 11, 12, 13(6)
1405	903	23	60	Durra		on 11, 12, 1(6)
1406	904	24	80	Durra		on 14, 15(6)
1525	1033	25	65	Durra		on 11, 12, 13, 14, 15(6)

*fl. = flowering

container. Even after several hours these heads, full of pollen, could be used to cross-pollinate seed parent heads.

Dehiscence will occur shortly before or after daybreak, following warm dry nights. If there is high humidity or dew, dehiscence may be delayed until 9 or 10 a.m. Dehiscence of anthers on cut heads will occur at essentially the same time as on the heads remaining on the plant. Using Webster's procedure, each head was used twice, and two heads were used per pollination. One pollinator head was held in each hand; these were wiped several times from bottom to top of the seed parent head. The seed parent head passed between the two pollinator heads. By this technique, the average seed set rose from about 5 to 40 g per cross. An estimate of the quantity of seed expected per pollination is necessary to determine the number of crosses needed to produce the seed for the yield trial program.

If Webster's technique is used and many combinations are to be made, the number of each kind of pollination should be determined on the day before pollination. This can be done by counting the number of appropriate seed parent heads, then marking the seed parent bags so that they can be readily located in the field the next day. Placing a paper clip at the top of the bag makes a convenient mark and it can easily be removed. It is best to use paper clips to close the bags, rather than staples, since the bags must be opened for inspection to determine when the head is ready for pollination, and to make the pollination.

A tabulation can then be made of how many crosses are to be made using a specific pollinator, and the appropriate number of heads can be collected. This procedure helps avoid making too many pollinations with one parent, or making too few with another, or missing a combination altogether. Experienced workers can count the heads ready for pollination while a technician keeps records. The person in charge of the crossing program should determine the crosses to be made; he must have a thorough knowledge of the field. The supervisor should assist in making the crosses and in collecting the information required to establish the next day's crossing program.

Male-sterile heads should be head-bagged just after the tip of the head begins to flower. The flowering tip is cut off and the head bag placed; the date is written on all head bags. If this technique is followed, the search for receptive heads is simplified. It takes 3 to 5 days for a head to flower fully. Thus, for example, almost all heads bagged on August 10 would be ready by August 15; therefore, only head bags marked August 14, 15, and 16 would require inspection on August 15 to find heads ready for pollination on August 16.

Teamwork for Crossing: Crosses can be made most efficiently by a crew working as a team. A technician can remove the bag from the receptive head and indicate the cross to be made while a worker wipes the pollinator heads several times over the seed parent head. The technician can then replace the bag and staple it shut. If labor is plentiful, one worker can carry the container of heads, and another can staple the bags shut. It is usually best to make all pollinations involving a given pollinator and then move to another pollinator, rather than to use several pollinators on the same seed parent and then move to a different seed parent. The increased handling of the containers involved in the second technique may increase error (there is a chance that the wrong box will be picked up or the wrong cross marked on the head bag).

Crossing of an A-line by a B-line to maintain A-line seed is done in about the same way that is used to cross an A-line with an R-line to produce a hybrid. However, the increase of A-line seed is easier, because the A and B-lines will be nearly synchronous in flowering.

Developing New Male-Sterile Seed Parents

Backcrossing is a breeding procedure used to transfer a desirable trait from a source (nonrecurrent) line to a desired (recurrent) line that does not have the trait. An important backcrossing program in sorghum breeding is the development of new pollen-sterile lines to be used as seed parents in hybrid programs. This backcrossing recovers the phenotype of the recurrent parent, but it is recovered as a male-sterile. Assume, for example, that it is known that IS 534 is nonrestoring when crossed onto male-sterile Combine Kafir 60 (A-line). Paired crosses should be made (numbering the parent plants in each cross and head rowing) during the backcrossing process to avoid problems of partial fertility. The use of an off-season nursery could double the speed of the backcrossing program.

Potentially useful nonrestoring lines for backcrossing can be identified in hybrid yield trials. Head bags should be placed on 10 plants in each entry of one replication of hybrid yield trials before flowering occurs. This is to determine whether the pollinator is nonrestoring (no seed set), partially restoring (partial seed set), or completely restoring (full seed set) in the different seasons and locations

in which the hybrid may be used in yield trials. One row of each parent should be sown at each location of a statewide or regional yield trial to accumulate flowering information that will be of later value to the seed producer.

Nonrestoring lines with good combining ability can be identified from such trials. Such lines offer promise in making new male-sterile seed parents. As the backcrossing procedure continues, partial fertility may appear and the chance of obtaining a new seed parent is lost. This can be avoided by numbering individual crosses and backcrossing only to completely sterile progeny. Consider the following crossing sequence, where NR = the nonrecurrent parent (male-sterile), and R = the recurrent parent (male-fertile). Heads on the NR rows are not head bagged until the tip of the head begins to flower (this exposed tip is cut off just prior to bagging). If any anthers appear with viable pollen, the head is not bagged. This procedure saves time, because only completely sterile heads are covered. If this is not done, all bags must be opened to search for a good sterile head at the time of pollination—a time-consuming process.

A breeding process for developing male-sterile lines is presented in Table 4.18.

Usually after three or four generations of this procedure, individual plant crosses need not be continued, and further propagation can be done on a row basis. This decision can be based on the degree of sterility of the NR row; i.e., if every plant in the row is completely sterile, individual plant crosses probably need not be made. There have been a few instances where it was not possible to eliminate partial sterile plants after five or six generations of numbered crosses. It is suggested that such pairs be dropped. A pocket magnifier is useful to decide if rudimentary anthers on some entries might contain viable pollen. Yield testing can be done to help eliminate entries after the second or third backcross. It may be desirable to continue the head-to-row procedure until uniformity is reached.

Male-sterile varieties vary in the ease with which seed is set. Some male-sterile varieties may have only a partial seed set when allowed to open-pollinate, whereas others set full seed under the same conditions. A hybrid is valuable only if it can be economically produced for farmer use. Seed producers will get better yields (hence produce at lower cost) from their production fields if good seed sets are readily attained. Selection of good seed parents can be made in the original selection; i.e., some entries in a yield trial will have scattered seed set while others will be fully set, except on the bagged heads. Pedigrees can be identified from entries with the best seed set on unbagged heads (and no seed set on bagged heads) to be made into male-sterile seed parents.

The crossing procedure outlined above can best be done by a well organized crew: two technicians and a laborer make a good team. One technician collects pollen for crossing and makes the self-pollination; the laborer transfers the bag of pollen to the other technician, who makes the cross. Each closes and staples the bags.

Crosses should be set up on the day previous to crossing. A technically trained person selects heads in the NR row for crossing and marks the bag in some obvious way (e.g., a paper clip placed at the tip of the bag). He then identifies a suitable plant to use as pollinator and marks it. It is easier to mark the row and pollination numbers on the bags at the time of pollination.

Crossing in Large Isolated Open-Pollinating Blocks

Testcrossing

If many male-sterile types are to be evaluated in combination with a few tester parents, it is possible to make the crosses in isolation. It is suggested that testcrossing begin with fairly uniform F_3s or with the F_4 generation. One isolation would be required for each pollinator (tester) parent, i.e., any number of male-sterile parents could be included in the same isolation, but only one pollinator. Several sowings of the pollinator parent would be required to assure that the *nick* (the simultaneous flowering of both parents in a cross) is achieved on all seed parents. Isolated crossing blocks might be planted two rows of pollinator to four rows of male-sterile or one row of pollinator to two rows of male-sterile. Staggered plantings of the pollinator should not be made within the same row, or pair of rows, but between rows or pairs of rows. If one row of a pair is sown late, it may suffer in development from competition with the first sown row, and probably would fail to flower at the desired time.

Testcrossing of both B and R lines is suggested; however, the crossing of B-lines on tester A-lines will result in male-sterile hybrids. It is therefore important to sow two rows of a mixture of male-fertile plants of different maturities after every six rows of testcrosses.

Seed Production

Uniformity of cultural practices is a key consideration when crossing is attempted on large isolated

fields. For example, variation in soil fertility and moisture content can cause differential response between the parents, thus failure to achieve nick. Plant protection must also be very good, as there may be differential susceptibility to insect attack. Care is necessary to insure that newly introduced parents of hybrids can be produced in the new area, before the hybrid itself is recommended.

If it is apparent that nick is not going to occur, selective use of nitrogen fertilization and irrigation water can bring the parents nearer to the same flowering date. For this reason, it is advisable to sow crossing blocks on fields shaped for furrow irrigation and to use a 2:4 or 2:6 ratio of pollinator to seed parent. After experience is gained, it is possible to determine the probability of nick even when plants

Table 4.18: Crossing and backcrossing identifying specific plants of both parents.

Season	NR	R	NR	R	NR	R	NR	R	NR	R
1	×	×								
	× -2	×								
	× -3	×								
	×	×								
	× -1	×								
Nur. row no.	25	26								
2	× -2	×	×	×	×	×				
	×	×	× -3	×	×	×				
	× -4	×	×	×	×	×				
	×	×	× -4	×	×	×	Plant in row			
	× -3	×	×	×	×	×				
	×	×	× -2	×	×	×				
	× -1	×	×	×	×	×				
	×	×	× -1	×	×	×				
	× -5	×	×	×	×	×				
Origin	25-1× 26-1	26-1	25-2× 26-2	26-2	25-3× 26-3	26-3				
Nur. row no.	81	82	83	84	85	86				

Note that this is a head-rowing process so that selection for agronomic superiority can accompany the development to new male-steriles. In this example assume that row 84 is inferior, so is discarded, and that row 85 was partially fertile. Note that no crosses were made into row 85 but that selection against row 84 was made at maturity (after pollination) when its agronomic characters could be fully judged.

3	×	×	×	×	×	×	×	×	×	×
	×	×	×	×	×	×	×	×	×	×
	×	×	×	×	×	×	×	×	×	×
	×	×	×	×	×	×	×	×	×	×
	×	×	×	×	×	×	×	×	×	×
	×	×	×	×	×	×	×	×	×	×
	×	×	×	×	×	×	×	×	×	×
	×	×	×	×	×	×	×	×	×	×
Origin	81-1× 82-1	82-1	81-2 × 82-2	82-2	81-3 × 82-3	82-3	81-4 × 82-4	82-4	81-5 × 82-5	82-5
Nur. row no.	45	46	47	48	49	50	51	52	53	54
etc.										

are quite young. If there is some question about the nick at this stage, the floral initial can act as an indicator. Floral initiation begins about 20 to 35 days after emergence in adapted varieties. The floral initial can be observed when the plants are 3 or 4 weeks old by carefully dissecting the stem. If the floral initials in the different parents are very different in sizes, selective use of water and nitrogen should begin promptly, favoring the late parent. (Application of water and/or nitrogen causes earlier flowering.) If the pollinator is late, water should be entered only into the furrow between the two pollinator rows. Nitrogen can be sprayed on the plants in the form of a 10% urea solution or placed in the ground. Neither parent should suffer, especially the seed parent, as yield would be lost. However, by careful application of water and nitrogen, the time to flowering can be altered by 7 or more days.

If observations of the seedling stage indicate that the nick is going to be very badly timed, the top two or three leaves of the earlier parent can be clipped. Some experience is required to know how much delay would be achieved for a given amount of clipping.

If a poor stand is obtained in the pollinator parent, or if the nick is bad, each morning during the pollination period an empty backpack duster (motorized) can be taken to the field to blow pollen from the pollinator heads directly into the seed parent heads. If nick seems highly unlikely, hand pollination may be necessary and may be worthwhile in small production fields where labor is readily available. A breeder with many different steriles in the same isolation may find that some hand pollinations are required if good seed sets are to be obtained on all combinations.

Seed yields from production fields on male-sterile CK60A commonly have varied from 50 to 300 kg/ha on the first few production fields attempted, then increased to 600 to 1000 kg/ha, and finally reached 1500 to 2500 kg/ha when the producers were more experienced.

Some evidence suggests that seed set can be enhanced by spraying only the pollen parent heads with boron. The rate used was 65 g of Borax per 200 gallons per ha, sprayed on the pollinator heads only.

Flowering Records

Preliminary hybrid trials will probably be grown in only one or two locations in a country. Advanced trials usually are grown widely throughout the country at experiment stations, and if possible, on farmers' fields. At each location that a hybrid trial is grown, the parents of each entry should be sown as a small nursery to obtain the days to 50% flowering. When these data are obtained over many seasons and locations, a good estimate of time to flowering will be available when a hybrid is released. This information is very valuable to the seed producer, who may need to stagger-sow one parent after the other to synchronize flowering.

Composites

Breeding for population improvement generally involves recurrent selection techniques. The usefulness of population breeding to sorghum improvement and illustrations of recurrent breeding techniques are the subject of this section. Composites of corn and pearl millet are potentially of value for direct farmer use. However, composites of sorghum continue to have a ragged appearance and would not be attractive for direct farmer use. Possibly, this problem may be avoided by making the composite from entries with similar head configuration.

Composites are useful to the sorghum breeder as a continuous source of new entries for the breeding nursery. Entries can be chosen for inclusion in a composite based on yield trial results, broad environmental adaptation, plant type, disease or insect resistance, some quality trait, drought tolerance, etc. It is very important that entries chosen be carefully evaluated before inclusion in a composite. Any number of entries can be included in the composite, and new varieties can be added at almost any time. A composite might be a single diverse varietal type or progeny from a single cross—or several hundred entries might be included. The number selected will vary with objective, but generally 10 to 20 carefully chosen parents appears to be a satisfactory number for most purposes.

When adding entries, care must be taken that the composite remains balanced: for example, equal amounts of seeds of the composite should not be mixed with equal amounts of seeds of an entry to be added. If the composite is in early stages of development, possibly 5 to 10 g of seed of the new entry could be mixed with 1000 g of the composite. If the composite has been advanced through several cycles of selection, then it is advisable to cross and backcross the new entry by the composite. If the progeny are felt to be contributing, they can be mixed as one of the selected entries prior to recombination. It is also possible to develop a "sidecar" in which the original composite is crossed onto the

new source and backcrossed as the recurrent parent. Selection is continued in the original composite and in the sidecar, so that both populations are improved simultaneously. The eliteness of the original composite is preserved with this technique.

Random mating at very low selection pressure should be done for about three generations after the entries have been mixed. This permits recombination between traits (breakage of linkage groups) before selection begins. Extremely poor plants can be discarded at this time, but about 90% of the population should be advanced to the next generation. There should be 2000 or more plants when the population is grown.

If a hybrid program is planned, a determination should be made as to whether a variety will produce a fertile or male-sterile hybrid following a cross onto a cytoplasmic male-sterile source; i.e., to determine whether the variety is a B-line or an R-line. Nonrestoring types (B-line) can be combined into one composite and restoring types (R-line) combined into another. Subsequently, selections from these two types of composites may form useful parents for hybrids.

Sorghum is primarily a self-pollinated crop, and most sorghum breeders prefer to incorporate one of the single recessive genes for male-sterility into the composite (this mechanism for male-sterility differs from the cytoplasmic system mentioned earlier). The ms_3 gene is most frequently used for this purpose, although ms_7 and *al* (antherless) genes are also useful. Genes at other loci cause male-sterility, but those cited above provide good expression of male-sterility in many environments.

Male-sterility can be incorporated most easily when the composite is being made. Each entry is crossed to the male-sterile source. Pollen from several heads can be used per cross. The F_1 will be fertile, as these factors for male-sterility are recessive. The F_1 should be self-pollinated, and a backcross can be made on the male-sterile segregates. The lines to be entered into the composite are the recurrent parents. One or two backcrosses should be adequate before the entries are mixed. If a composite is used as a source of male-sterility, the genetic background is more diverse than if a variety is used as a source; generally, this would be desirable.

The genetic factors for tallness and lateness are dominant; therefore a population of interbreeding plants will tend to become tall and late. Selection pressure to prevent this should be practiced (if required), particularly after completion of the three generations of recombination. It may be useful to remove very tall and very late types during this three-generation period. Tall and undesirable plants should be cut away before they shed pollen, thus preventing transmission of their genes into the population.

Normal and male-sterile heads cannot be identified at maturity. During the backcrossing period, while sterility is being introduced, the parent contributing male-sterility can be sown in one block and the entries or a mixture of the entries to make the composite (pollen parents) sown in another. The male-sterile plants can be identified by tags placed on the peduncle at flowering time. If maturity is important, the date of flowering can be written on these tags.

Plants in a new composite usually do not have the stature of selected lines. If elite similar-type varieties were used, the composite could be expected to be more uniform, and initially more robust, but the genetic diversity in the population would be small. If large numbers of diverse entries were added, the population would not be as uniform and parents would not be as robust; but the genetic diversity would be great. The breeder's objectives determine how a composite is to be made. The overall yield of a composite can be improved by cycles of selection, thereby improving the population as a source of new breeding stock for the nursery, and possibly for direct farmer use.

Symbolic Designations of Sorghum Populations

Sorghum breeders meeting at the University of Nebraska in 1970 developed a system of symbolic designations for populations. This system was later approved at the Seventh Biennial Sorghum Research and Utilization Conference, Lubbock, Texas, in March 1971. The system, presented in *Sorghum Newsletter*, is essentially as follows:

- A brief designation of station, state, province, or country.
- The letter "P," used to indicate that these are populations.
- Inclusion of the letters "B," "R," or "B and R," to indicate whether the population is made of lines that are restoring (R) or nonrestoring (B) on cytoplasmic male-sterile lines, or whether they are a mixture of such lines.
- A designation, in parenthesis, of the breeding system. Proposed symbols are as follows:
  - M = Mass selection
  - H = Half-sib family selection
  - F = Full-sib family selection

S = Selfed progeny evaluation
R = Reciprocal recurrent selection
FR = Reciprocal full-sib selection

- The symbol "Cn" appears last, "C" indicating cycle and "n" indicating the number of the cycle.

As an example of the system, NESP 1 R (M) C3 would indicate population one of the Near East Sorghum Improvement Program. The population has the R-line reaction and is in the third cycle of mass selection.

When a population is sent from one station to another, the receiving station should attach its own symbols after selection has begun. The station providing the composite should be acknowledged when the receiving station distributes the population to others. This will give credit to those who have contributed and will help to preserve a breeding history.

Selection Techniques

After a composite has been formed, and random mating with low selection pressure has occurred for about three generations, the composite can be advanced by selection for any number of traits of interest. The selection process is cyclic, involving a testing or evaluation phase, and a recombination phase—the term "recurrent selection" generally applies.

A number of breeding systems have been used (these are listed above with their symbolic designations). Variations are possible for any of these systems. The system used will depend on a number of factors; for example, heritability of the trait. Mass selection is effective for traits with high levels of heritability and is comparatively less useful if the heritability is low. The number of generations per year, labor and financial resources, the level of outcrossing, and the use of genetic sterility may all be important factors in choosing a breeding system for composites. Each of the breeding systems is described below.

(Note: When yield testing is a part of the breeding system, fewer replications at several locations are more useful than many replications at one location; for example, two replications at three or four locations rather than four replications at one location. This allows selection of entries that are more stable in their performance in different environments.)

Mass Selection

This technique is easy to use and is effective, particularly if the trait of interest has high heritability. It is useful if a population is highly heterogeneous. Lonnquist (1964) has listed the advantages and disadvantages of this system. Each cycle is one generation, whereas other systems require more than one. A large germplasm pool can be sampled (any system requiring yield trials presents a limit on the number of samples that can be evaluated). The most obvious limitation to mass selection is that it is a phenotypic selection made in a single sowing. Phenotypic selection may not be effective genotypically, particularly after several cycles of selection when plants in the population perform similarly and well.

When the mass selection system is used, plants should be widely spaced and should not be sown at the rates recommended for commercial crops. Since selection is based on individual plant phenotype, each plant should express its maximum potential.

Doggett (1972) has described two systems of mass selection: (1) Seed was harvested from only selected male-sterile plants. These seeds were bulked and sown to form the population for the next cycle of selection. (2) Male-sterile plants were selected in one cycle, and male-fertile plants in the next cycle. The next cycle of selection was made on only male-sterile plants, etc., in alternating fashion—the system is referred to as "alternating choice."

Half-Sib Family Selection

This is a simple system to use in a sorghum population in which genetic male-sterility has been incorporated (Gardner 1972). Male-sterile plants in the population are tagged at the time of flowering and are permitted to open-pollinate. Each head is harvested and threshed separately, the seed from one head forming one entry in a yield trial (evaluation phase). Remnant seed is saved. The best entries are chosen from the yield trial results, and remnant seed of these entries is bulked and sown—this population forms the recombination phase. Again male-sterile plants are tagged and harvested individually to form the next cycle of evaluation. This method of selection is known as "half-sib family selection" because only one parent in the cross is selected (i.e., the male-sterile plant). Since the selected male-sterile plant is open-pollinated, the pollinator parents are not known. Each harvested head forms one family.

Lonnquist (1964) and Webel and Lonnquist (1967) describe a modified ear-to-row procedure in corn that amounts to a half-sib family selection system. They began with the open-pollinated variety of

corn "Hays Golden." Plants within the open-pollinated variety were randomly chosen and crossed—each crossed ear providing a full-sib family for testing (both parents selected or known). Each full-sib family formed an entry in a replicated yield trial, and the top 20% were selected. Remnant seed of the selected families was planted in a crossing isolation, a bulk of the selected families being used as the pollinator parent. The progeny (family) rows were detasseled, and at harvest ears were taken from the five best plants in each row. A total of 219 ears, 5 from each of 43 families, plus 4 from other families, provided the base to form the population each cycle. Each ear represented a half-sib family (pollinator not selected). The half-sib families were sown in a 15 x 15 triple lattice at three different locations; the original open-pollinated variety and a double cross hybrid were included. The plots were 1 x 8 hills, four seeds sown per hill and later thinned to two plants.

One test location was set as a yield trial with crossing block. There were four plots of females and two of males in alternating fashion. The male rows were from a mixture of equal quantities of seeds from the 219 selected ears. At flowering time, the female rows and the open-pollinated variety and hybrid checks were detasseled. At harvest, five selected ears were put in a separate bag and weighed with the bulk harvest of the plot. Seed of the five ears from each of the best 44 families selected produced the half-sib families for the next cycle.

Eberhart (private communication) has outlined a breeding procedure for sorghum composite KP5(s) developed by Jack Cassady at Kansas State University, USA, to improve yield and disease and insect resistance. The breeding system involves half-sib selection, mass-selection, and S_1 selection for yield traits. Eberhart points out that this system is very efficient for a self-pollinated crop such as sorghum if genetic sterility is available. The steps in each cycle are outlined below:

1. Bulked seed from sterile plants was sown in isolation. Six hundred male-sterile plants (half-sib families) were selected and threshed individually.
2. These 600 half-sib families were screened in the seeding stage for downy mildew and greenbug resistance. Downy-mildew-resistant plants were transplanted, and half-sib families that were resistant to greenbug and downy mildew were sown from remnant seed. One thousand male-sterile plants were selected at harvest.
3. The seed from these 1000 plants (half-sib families) was planted head-to-row, i.e., the seed from one plant was planted in one row in a nursery. This was done in an off-season nursery in Puerto Rico. At harvest, one fertile head from each of 500 rows was selected. Selection was made in rows (families) showing greenbug and *Periconia* resistance if ratings for these traits were available at harvest time, i.e., if the infections developed during the season so that selection was possible. If ratings were not available, agronomically desirable plants were selected for both grain and forage. Each fertile head formed an S_1 family.
4. Using a second generation in the off-season (February to March), the 500 lines (selfed, fertile S_1 plants) were evaluated for downy mildew resistance. A 10 x 10 simple lattice was used for lines 1 to 100 and a single replication was used for the remaining 400 lines. Two hundred S_1 families with the greatest downy mildew and greenbug resistance were selected for S_1 yield trials.
5. In the regular growing season S_1 yield trials were conducted with 200 S_1 lines in two 10 x 10 simple lattices at two locations. Ten lines from each trial were selected (S_1 family selection).
6. The same 500 lines were planted in a maize-dwarf mosaic (MDM) virus nursery, using 10 x 10 simple lattices with one replication in each of two locations. The 5 to 15 lines with the greatest MDM resistance (not selected in yield trials) were selected for inclusion as MDM-resistant lines in the next cycle.
7. The same 500 lines were planted in an anthracnose nursery (regular planting season). Five to 15 resistant lines not selected in yield trials were selected for inclusion as anthracnose-resistant lines in the next cycle.
8. The same 500 lines were planted in the Texas Downy Mildew Nursery (field resistance). Five to 15 resistant lines not selected in yield trials were selected for inclusion as downy-mildew-resistant lines in the next cycle.

(The mass selection for disease resistance as indicated in steps 6, 7, and 8 can be omitted if disease problems are not important—they slow down the rate of gain for yield.)

9. The same 500 lines were planted in the regular breeding nursery. Fertile plants were tagged, and the best 20 rows at harvest were selected.
10. Approximately equal numbers of seeds were

bulked from each of 10 selected plants from 20 S_1 lines selected for yield (Step 9). Seeds of the MDM, the downy mildew (field resistance), and the anthracnose selections were bulked separately. These bulks were planted in one isolation (off-season) in alternating rows: yield, MDM, yield, downy mildew, yield, anthracnose, yield, MDM, yield, etc. Sterile plants were tagged, and 600 were selected at harvest (half-sib families) to begin the next cycle. Three hundred were used for yield trials, 100 for MDM, 100 for downy mildew, and 100 of the half-sib families for evaluation for resistance to anthracnose. This began the second cycle of selection.

If selection is for resistance to a particular disease or insect—or for a quality characteristic or similar trait—the following system may be useful (the system described is for the sorghum composite KP2 (SD) developed by Cassady):

1. Plant 1000 progeny from male-sterile plants (half-sib families) in an off-season nursery; at harvest save one fertile head from 500 good plants.
2. Plant 500 lines (head rows) in a downy mildew nursery (field resistance), using two replications for the first 100 lines and one replication for the others. Resistance is evaluated in the seedling stage.
3. Select 10% of the best downy-mildew-resistant entries and bulk remnant seed of these selections from the S_1 lines (from the selected fertile heads mentioned in Step 1). Sow the selected S_1 families (50) in isolation, and tag male-sterile plants at flowering. Harvest 300 male-sterile plants (half-sibs, both forage and grain types), thresh individually, and send to the off-season nursery to begin the next cycle. After the first cycle, possible fertile heads need be taken from only 100 or 200 plants per cycle rather than 500.

Full-Sib Family Selection

The use of male-sterility in sorghum composites permits selection by the full-sib family system. A full-sib family can be formed by crossing a selected male-fertile plant with a selected male-sterile plant. The full-sib families should be evaluated (yield trial), and remnant seed of selected families should then be bulked to allow for recombination. Crosses of male-fertile plants are then made, and the cycle is repeated (Gardner 1972).

A full-sib family selection system in maize has been described by Moll and Robinson (1966), who used three different populations: two open-pollinated varieties (Jarvis and Indian Chief), and an F_2: (NC7 x CI21) F_2. The breeding procedure was the same for all three populations. The families to be tested were formed by crossing randomly chosen plants as male parents—each to four plants used as females (forming four full-sib families for each male parent).

These families were divided into sets of four male groups (16 families) and entered in yield trials with two replications. Remnant seed from the highest yielding families was planted in a nursery to provide the population for the next cycle.

The population was made up as follows: single plant-to-plant crosses were made so that members of a single family were crossed with members of eight other families that were unrelated to the single family. Approximately equal numbers of members from each family were used in crosses between families.

This system can be illustrated as follows (assume that the population (NC7 × CI21) F_2 was used):

Male plants chosen at random		Female plants
1	×	a, b, c, d
2	×	e, f, g, h
3	×	i, j, k, l
4	×	m, n, o, p
5	×	q, r, s, t
n		

1 × a was a full-sib family; sets were formed:

1 × a, 1 × b, 1 × c, 1 × d
2 × e, 2 × f, 2 × g, 2 × h
3 × i, 3 × j, 3 × k, 3 × l
4 × m, 4 × n, 4 × o, 4 × p

This set was sown as a yield trial with two replications.

Remnant seed of the highest yielding families (1 × a, 1 × b, etc.) was planted in a subsequent nursery to be used in forming the population for the next cycle.

Again, single plant-to-plant crosses were made so that members of each family were used in crosses with eight other families. Approximately the same number of members of each family were used in a cross between families.

Assume that the following families were selected from yield trials:

1 × a, 1 × c, 2 × f, 3 × j, 3 × e, 3 × l,
4 × m, 4 × n, 5 × r, 5 × s, 5 × t.

Then single-plant crosses were made as follows:

(1 × a) × (2 × f)	(1 × a) × (4 × n)
" × (3 × j)	" × (5 × r)
" × (3 × l)	" × (5 × s)
" × (4 × m)	" × (5 × t)

The same number of crosses (say three) was made for each combination between two families; i.e., three individual plants of (1 x a) would be crossed with three individual plants of (2 x f), of (3 x j), etc.

Individual plant pedigrees were kept so that the record book might appear as follows (assume that plants in the nursery row were numbered):

(1 × a)-1	×	(2 × f)-5
(1 × a)-3	×	(2 × f)-2
(1 × a)-12	×	(2 × f)-10
(1 × a)-21	×	(3 × j)-15

(where the -1, -5, -3, etc. are the number of the plant in the plot).

Crossing was done so that inbreeding was minimized (i.e., the cross (1 x a) x (1 x c) was not made, because the parent 1 was common). Crosses were made so that there were no common parents.

These crosses were placed in yield trials; i.e., (1 x a)-1 x (2 x f)-5 is one full-sib family and formed one entry in the trial; (1 x a)-3 x (2 x f)-2 was in another plot, etc. At the same time, seed from ear (1 x a)-1 x (2 x f)-5, was sown in a single hill to provide seed of entries selected for the next recombination nursery in the next cycle.

Selfed Progeny Evaluation or S_1 Family Selection

S_1 family selection is one of the most effective selection schemes for sorghum (Gardner 1972). Heads of male-fertile plants can be bagged at flowering time to insure selfing, or they can be tagged to be sure that male-fertile (and not male-sterile) heads are harvested at maturity. Selected plants are harvested and threshed separately, each head forming an S_1 family. These families are entered into yield trials. Remnant seed from the selected families, based on yield trials, is sown, and seed from male-sterile heads is selected to insure recombination. Seeds from male-sterile heads are then bulked and sown. Male-fertile heads of good plants are identified for testing to begin the next cycle.

Doggett and Eberhart (1968) have described a system for selecting composites in Uganda, where the rain pattern permits two crops. Two populations were described: Population 1 was homozygous for the genetic restorer factors for cytoplasmic sterility. This population was made of 121 lines crossed and backcrossed to ms_3. Population 2 was made up of nonrestorer B-lines: 101 good B-lines were crossed and backcrossed to an ms_3 source.

A nursery of 800 or more entries from each population was sown at one location during the first rains. Thus, 800 or more entries came from male-sterile heads in population 1, and 800 from population 2. Entries were grown in blocks of 20 to 40 entries to reduce environmental variation. A head from a good male-fertile plant (S_1 family) was selected from the best 30 to 50% of the head rows (these were taken as selfed heads because of the low outcrossing percentage).

Trials with two or three replications, and with 400 or more entries, were grown at as many locations as possible. Remnant seed of each S_1 family was saved and increased, if necessary, and the highest yielding 10 to 20% of the entries in the yield trials were identified.

Remnant seed of selected S_1 families was mixed and sown in bulk. Male-sterile heads were identified and tagged. Undesirable fertile plants were removed before pollen shed. Selection was among tagged plants at harvest; these selections began the next cycle.

With this system, superior S_1s can be taken from the population at any time and advanced as lines by a pedigree selection system. New material can be added to either population at any time by mixing with the selected bulked S_1 seed prior to recombination or by backcrossing and mixing selected progeny with bulked S_1 seed.

A male-sterile population (2-A) could be developed at any time by crossing and backcrossing the population 2B to a cytoplasmic male-sterile source. If a hybrid program is of interest, entries from population 1 could be crossed to population 2-A. S_1 families in population 1 selected for recombination in the next cycle would be based on yield trial results of these crosses.

Recurrent Selection

The term "recurrent selection" describes cyclic systems of selection in composites. The terms "mass selection," "half-sib selection," etc., refer to particular selection processes, but these processes are forms of recurrent selection. Several forms of selection under the heading of recurrent selection can be described, all using the following procedure:

1. Good plants are selected from an intercrossing population and selfed for one generation in a nursery.
2. The same plants are crossed onto a tester (top-cross) and evaluated for yield and any other characteristics of importance. The crossing can be done in the same generation as the selfing.
3. Remnant selfed seed of selected lines based on the top-cross are intercrossed.
4. The cycle is repeated.

If the tester for the top-cross were the bulk population from which the selfed lines were derived, the test would be for general combining ability. If the tester were an inbred line, the test would be for specific combining ability. The term *general combining ability* is used to describe plants or populations that can be crossed to an array of other plants or testers (of differing genetic background), with good performance for all the crosses. The term *specific combining ability* is used to describe plants or populations that perform well when crossed to an inbred line; i.e., a *specific genetic entity*. (Their general performance may vary, performing well on some inbred line testers but not on others.) These terms have relevance only in relation to hybridization. Any line or variety may have good general and specific combining ability when hybridized, but when used as lines or varieties per se, the terms are not relevant. In sorghum (in a population in which genetic sterility has been incorporated) the test would be for general combining ability, and it would probably be some form of half-sib family selection.

Reciprocal Recurrent Selection

A breeding program using reciprocal recurrent selection implies the existence of two populations, each serving to provide source material to advance the respective populations and to serve as a tester for the other population. Individual S_0 (F_1) plants in population A would be self-pollinated and simultaneously crossed to several plants of population B. In the same way, individual S_0 plants in population B would be selfed and simultaneously crossed to several plants in population A. This provides the material for two sets of testcrosses. Seed from S_1 plants (selfed S_0 plants) selected in the testcross trial would be intercrossed; the S_1 plants from population A forming a new population A_1 and those from population B forming a new population B_1. The cycle is then repeated. The ultimate goal of this system is to produce commercial hybrids between lines derived from the two populations. This can be done at any stage of breeding—ranging from crossing between the populations to crossing between inbred lines derived from the two populations.

The characteristics of the two populations in sorghum might be as follows:

Population A - To develop R-lines (or pollinator parents in a hybrid program):
- Genetic male-sterility
- Either type of cytoplasm
- High frequency of cytoplasmic fertility restoring genes (from R-lines)
  or
- Cytoplasmic male-sterility
- Sterile cytoplasm (A-line)
- Optimum frequency of cytoplasmic restoring genes (R-lines; review section on production of hybrid sorghum if the terminology is not familiar).

Population B - To develop B-lines, i.e., the maintainer lines for the seed parents (A-lines) of hybrids. B-lines do not restore male-fertility to the progeny of crosses with A-lines:
- Genetic male-sterility
- Fertile cytoplasm
- High frequency of nonrestoring genes to cytoplasmic male-sterility (from B-lines)

Random recombination for three generations with low selection pressure is first undertaken as discussed earlier in the section. Male-sterile plants are chosen to begin the population that will form the basis for the reciprocal recurrent selection program. A cycle of selection would be as follows—

Step 1:
- (a) Select among fertile plants in population A (tag or bag these plants for identification at harvest).Cross the same fertile plant to several male-sterile heads in population B.
- (b) Select among fertile plants in population B and cross with several random steriles in population A. (Note that identification of the fertile plant and its crosses onto male-steriles must be maintained).

Step 2: Conduct yield trials; two replications in several different areas. If cytoplasmic male-sterility is used in population A, male-sterile plants will appear in the trial. It is necessary to insure that there is an adequate amount of pollen in the field throughout the flowering period of the trial even if a heterogeneous pollinator is sown as a pollen source.

Step 3: Based on yield results, seeds from selected fertile plants (steps 1a, 1b) are bulked and grown in isolation. Allow for random pollination on male-sterile heads.
Mark male-sterile plants at flowering time (use tags or paint from an aerosol can).
Harvest seed from male-sterile plants from each population A and B to form the new populations from which male-fertile plants would be chosen and crossed to tester plants in the other population.

Step 4: Repeat the cycle.

Techniques for Increasing Gain from Selection

The rate of progress (gain in increasing yield in a population) depends on a number of factors the breeder should be aware of for his particular breeding situation so that he can decide on the breeding system to use. Eberhart (1970) presents a discussion on this question in detail; salient features are outlined below.

One of the ways to increase the gain in yield per cycle of selection is to increase the additive genetic variance; i.e., to increase the diversity of the entries going into a composite. Collections and breeding material from many places in the world can be used to increase diversity.

The rate of gain can be increased by increasing the selection intensity; i.e., by taking a fewer number of the very best entries in a composite to re-form the composite in the next cycle. Most maize breeders select 20 to 40 lines for recombination each cycle. A problem arises (particularly where progeny testing is involved) in having sample sizes large enough to represent the diversity in a population. It may be desirable to have a broad-based composite under mass selection, saving 25 to 30% each cycle, so that the population under intensive selection could be intergressed periodically. This could be done by crossing steriles of the highly selected population with pollen from the broad-based composite. This intergression would be particularly useful when gain per cycle of selection begins to decrease.

Gain can be increased by using two or three generations per year. This can be done by using off-season nurseries: for example, by using a warm-weather location during a cold winter and/or using irrigation during a dry season. The breeding system used depends on the number of generations that can be obtained in 1 year; or, more generally, how rapidly each cycle of selection can be completed.

Improvement in plot technique is helpful in increasing gain per cycle. The better the crop, the more accurate the selection and, with proper technique, more entries can be evaluated. Techniques such as the following are useful:

- The yield trials should always be grown on fields that were uniformly cropped the previous year so that variations in the field are minimized.
- The crop should be well managed. Use high levels of fertilizer to reduce variability within a replication; irrigation, pest control, freedom from weeds are all important factors in obtaining good plant expression.
- The design of the yield trial may be important (with maize in Kenya, the use of the lattice design was found to be useful in removing some random variation statistically).
- The number of plants per plot is important (with the KCA maize composite in Kenya, there was very little increase in yield gain with more than 15 or 20 plants per plot (Fig. 4.1). More progeny rows can be tested if the plot size is reduced, enabling a better sampling of the population.
- When the genetic variation in the population is high, it has been found better to have a few replications at many locations than many replications at one location. (With the maize composites in Kenya, two replications at four locations were found to be efficient—the cost of conducting trials at more than four locations was not worthwhile compared to the gain in yield.)

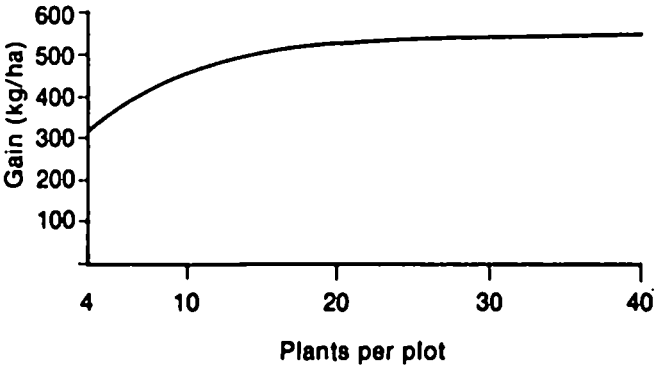


Figure 4.1: Effect of number of plants per plot on gain in yield.

This figure illustrates the relationship between gain in yields and number of plants per plot on a KCA maize composite in Kenya, two replications and four locations (Eberhart 1970).

A number of these points are illustrated in the following figures.

Note that the difference between expected gain illustrated by Figures 4.2 and 4.3 is only in number of generations per year 3 seasons in 2 years vs 2 seasons in 1 year. Note that the relative efficiencies of the full-sib and S_1 testing procedures are reversed when based on this difference in number of generations per year.

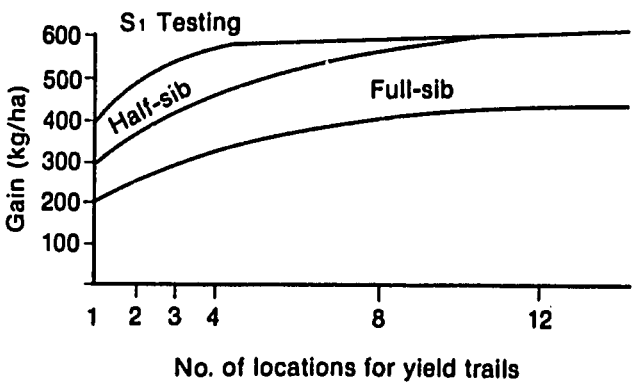


Figure 4.2: Effect of number of test locations on gain in yield - 3 seasons in 2 years.

This figure illustrates the expected annual gain in yield of the KCA maize composite with different numbers of test locations in Kenya using 3 seasons in 2 years (Eberhart 1970).

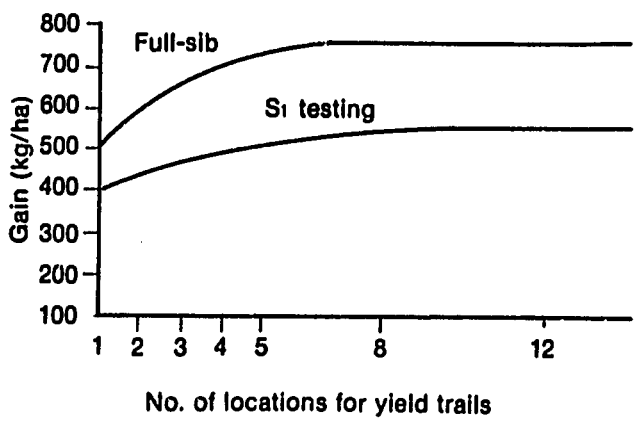


Figure 4.3: Effect of number of test locations on gain in yield - 2 seasons in 1 year.

This figure illustrates expected annual gain in yield of the KCA maize composite with different number of test locations in Kenya using 2 seasons per year (Eberhart 1970).

Breeding for Insect and Disease Resistance

Breeding is a process of changing a characteristic of a population over a number of generations by applying selection pressure on the population. A number of breeding techniques can be considered from a discussion of breeding for insect and disease resistance. Breeding for resistance requires a capability to routinely screen large numbers of lines in a crop improvement program.

The rate of change achieved depends on several factors:

- mode of inheritance and breeding procedures,
- ease of identifying the trait being selected for,
- intensity of selection pressure that can be applied, and
- environmental factors.

Mode of Inheritance and Breeding Procedures

The mode of inheritance refers to how a character is inherited—single gene, a few genes, many genes—and how much of the variation observed is due to additive or nonadditive effects (dominance and epistasis). Resistance to a race of wheat rust is an example of a single-gene mode of inheritance. Each new race of wheat rust usually requires that a new gene source for resistance be found; i.e., the relationship between host and parasite is quite specific, hence there are as many sources of resistance to deal with as there are races of the disease. Generally, it is possible to recover a varietal type resistant to a new race of rust, and one gene can be introduced into a genotype without greatly altering that genotype, except for the factor introduced.

Backcrossing is a method of gene transfer. The agronomically desirable type (recurrent parent-R) is crossed by the source of resistance (nonrecurring type-NR), and repeated backcrosses are made with the recurrent parent.

R × NR
(R × NR) × R
(R × NR) R × R, etc.

If the character in question is recessive, the F_1 (R × NR) will be susceptible. It therefore becomes necessary to self every other generation or so, to recover the character desired. For example, if the R-line were genetically SS for susceptible, and NR was ss for resistant, then the F_1 would be Ss, or susceptible.

The first backcross would be between Ss and SS parents, and the progeny would be one-half Ss and one-half SS. Plants from these seeds would be self-pollinated, and the next generation would then segregate 5SS:2Ss:1ss. Backcrossing would then continue by crossing the ss types by the recurrent parent and repeating this whole process until the resistant recurrent type was recovered (usually four to six backcrosses).

The number of backcrosses involved may be reduced if the R and NR parents are similar phenotypically (possibly of the same varietal background). Suppose that it is desired to transfer resistance into variety A_1 and many different varietal sources of resistance are available (A_5, B_2, C_7, D_{10}, etc.), then the best choice for the NR line would be A_5. The cross $A_1 \times A_5$ would be phenotypically much closer to the desired type than the cross $A_1 \times C_7$, thus fewer backcrosses would likely be required.

Fortunately, good sources of resistance are available for the major diseases of the sorghum crop; hence, a few good source lines may be found that can be used to evolve agronomically good and disease-resistant varieties and parents (see section on the genetics of sorghum).

If a hybrid is involved and all parents are susceptible, then it may be necessary to transfer the desired resistance into each parent. This would not be so if the resistance were due to a dominant factor; it would then be required (in the homozygous condition) in one parent. If the factor is recessive, then it must be entered into both parents (or all parents). Generally, an agronomically good hybrid is a cross between parents of diverse origin. Using the same source of resistance for both parents of the hybrid reduces this diversity and may reduce yield. Whenever possible, diverse sources of resistance should be used in a hybrid program.

The availability of simply inherited factors for resistance is convenient for breeding purposes. However, as in the case of wheat rust, the resistance may break down with a new race of the disease. Horizontal resistance is controlled by many genes, and while complete resistance may not be expressed, a good level of resistance is possible that generally remains more stable over a longer period of time than does the highly specific relationship expressed by the wheat-rust situation. From a crop-production point of view, horizontal resistance is valuable and is a potentially useful concept for the plant breeder.

It is worthwhile to screen collections of varietal types and breeding stocks for resistance and to study the inheritance of the desired trait in promising lines. Genetic diversity is as important to selection for resistance to insects and diseases as it is for yield. If the character is controlled by two, three, or four genes, the backcross method can be used and chances are reasonable that the resistance can be transferred to obtain a phenotype similar to the original with the resistance recovered. There may be a few genes of major effect whose expression is blurred by a large number of modifiers—genes of minor effect. It may be that one or more of the major factors would be dominant or partially dominant. A variety with resistance of this sort may be much easier to use than one controlled by a large number of factors, all with minor effect; i.e., if the mode of inheritance is quantitative. If this is the case, simple transfer of the characteristic by backcrossing is not possible. There is a random assortment of genes and it becomes impossible to find a recombinant with all the desired factors (the population size would be too great and the chance of identifying the specific individual in such a large population improbable). Generally, however, it is possible to backcross once or twice; then a new line must be selected by screening in segregating generations. It is not possible to recover the desired variety with resistance added. The employment of population-breeding techniques may be very useful.

Breeders hesitate to use unadapted landrance accessions from the germplasm collection in combination with elite breeding stock for the sake of a resistance trait. Clearly, there is a need to build resistance for a trait into good agronomic varietal material to make it more useful in the crop improvement process. It is useful to seek some balance between genetic diversity and uniformity. Screening of very elite breeding stock will likely have little reward because the genetic variability for the trait of concern will probably be so low that selection will have limited effect. On the other hand, screening in an F_2 generation may involve so much variable material that the job becomes cumbersome and decisions are made on single plant behavior, which may be of limited reliability. To a degree, the nature of inheritance of a trait will give some indication of how to manage it. On an average, it is probably best to begin evaluation of a resistance trait in the F_3 or F_4. However, in the F_2, obviously susceptible plants should be discarded.

There are three general approaches in a pedigree breeding procedure that one can consider in building resistance into agronomically good varieties. If heritability for resistance is very high—for example, with leaf rust—it may be possible to recover resistance while selecting for agronomic superiority. If heritability is somewhat lower, another approach is

to grow the same entry in the breeding nursery for agronomic evaluation and in a screening nursery for evaluation of resistance. It is best if cooperating scientists evaluate the material in both nurseries together. First, evaluation would be made in the screening nursery to identify resistant entries (families). Then, among the resistant families, agronomically good plants could be selected. These sister lines could then be evaluated the following year in both the breeding nursery and the screening nursery. This breeding procedure assumes that good levels of resistance are found in a reasonable number of entries—if not, the procedure outlined below should be considered.

If good levels of resistance are not found, or if gain for resistance has plateaued at a lower level than desired, it will be necessary to intercross between different pedigrees to increase genetic variability. If this does not work adequately, it may be necessary to introduce new source material into the program. The procedure involves an alternating breeding approach. This approach would most likely be used when heritabilities are relatively low but there is a reasonable level of additive genetic variance. It would be convenient to divide the material being developed into two units. One unit would be screened for resistance while the other unit would be evaluated for agronomic superiority in a no-stress situation. Good individual plants would be selected in both nurseries (pedigree breeding). Good plants in the screening nursery would be head-rowed the following year in the no-stress situation. Selections in this nursery would then be head-rowed in the screening nursery the subsequent year, i.e., the same material would be advanced alternatively one year in the screening nursery, one year in no-stress, the next year in the screening nursery, etc. One would not be making judgment in one nursery and selection in another, assuming that genes for resistance were in the set grown in the agronomic nursery. In this case, the plants showing resistance are advanced to a no-stress situation, and selected plants from this nursery go back to the screening nursery. This more nearly assures the breeder that the selection is carrying the genes for resistance. Crossing between selected entries, followed by selection, may be required to increase the gene frequency for resistance. It is quite likely that the primary selection pressure will have to be for the resistance trait, with agronomic improvement a second priority.

There are several population techniques that might be worthwhile, all involving some form of recurrent selection. The population might be made by combining good agronomic lines with good source lines for resistance. It is important that entries included in a population be selected carefully for the traits of interest. Random recombination with low selection pressure should occur for several generations before selection is begun to develop new lines. It may even be desirable to establish a population including many varietal sources (if only less-susceptible types are available to enhance the degree of resistance) before any effort is made to improve agronomically superior types. As more lines are added to make a composite, particularly if sources of resistance and of agronomic eliteness are both included, the expression of the resistance will likely diminish. The gene frequency in a population from a cross is the average of the gene frequencies of the parents; i.e., if line A has a gene frequency of 0.7 for resistance and line B has a gene frequency of 0.4, then the crossed population (A × B) has a frequency of 0.55. If line B had a frequency of 0.04, the frequency in A × B would be 0.370 (which is a lower base from which to begin selection).

Some of these population techniques are most useful with cross-pollinated crops or with crops that have a reasonable degree of cross-pollination. Sufficient crossing occurs in sorghum to justify establishing open-pollinating populations. However, recombination can be enhanced if hand pollinations are made (or better, if genetic male-sterility is introduced into the population). The population can be made one-fourth male-sterile and harvest taken only from male-sterile plants. All seed obtained would then be from a cross. The cytoplasmic form of male-sterility is used to make hybrids for commercial purposes. It is common practice and recommended that only a genetic source (ms_3 and/or ms_7) be used in composites.

If a polygenically controlled factor is to be used in a hybrid program, diversity in the parentage should be maintained. It may be desirable to make two unrelated populations rather than one. Reciprocal recurrent selection may be a very useful breeding technique in this case. If genetic sterility is introduced into unrelated populations, some thought might also be given to maintaining diversity in the source lines for male-sterility.

Recurrent selection involves an evaluation and a recombination phase. The evaluation phase would include evaluation in yield trials and in separate screening nurseries for one or more of the insect and disease problems of concern. Only the best selections from each evaluation test are included in the recombination phase (see section on Composites). Population breeding is useful for the simul-

taneous incorporation of several traits into agronomically good material.

If resistance is to be added to an already agronomically elite population, selections from the population can be crossed to the source(s) of interest. Progeny from these crosses should be evaluated in the F_2, F_3, and (if necessary) F_4 generations for both agronomic and resistance traits. Only when these progenies have an agronomic eliteness equal to the parent population are they incorporated; thus the gene frequencies for traits contributing to agronomic eliteness are not reduced.

A "sidecar" technique is employed by the maize program of CIMMYT. Bulk pollen from the population is crossed onto the source(s) of resistance. Progenies are then screened for agronomic and resistance traits. At the same time, improvement of the parent population continues. When good levels of resistance and agronomic eliteness are found in the progeny, a backcross is made using bulk pollen from the improved population onto the resistant progeny, and the cycle is repeated. This nonrecurrent population is a sidecar of the parent population. In this way the population is backcrossed onto the source; there is no chance of reducing gene frequencies for desirable traits in the parent population (in fact, they are being improved during the backcrossing process).

Ease of Trait Identification

The ease with which a trait can be identified is an important factor in breeding. The expression of a character may be influenced by both the genetic background and by the environment. A major gene for resistance may express itself well in variety A and poorly in variety B; i.e., variety B may carry a complex of modifying factors reducing the resistance effect of the gene in the B. The background effect on the expression of a trait would also be important in identification of varieties for genetic studies where good expression is important to the determination of the frequencies of individuals in the various groups in a segregating population. Choice of parents is important in a backcrossing program, as expression of resistance might vary according to the parents used. The identification of the best source to use for the improvement of a particular agronomically elite line may be worthwhile.

Breeding for resistance to charcoal rot is complicated because, as yields increase, there is often an accompanying increase in susceptibility to this disease. Apparently the increased translocation of metabolites to the grain contributes to increased susceptibility of the stem to infection (other stresses, such as drought also condition plants to susceptibility). Variability does exist, but it is not clear how far it will be possible to select for both high yield and a high level of resistance to charcoal rot.

Shoot fly is an insect problem that clearly demonstrates the complexity of the breeding situation. This is a severe pest on sorghum in India (the fly maggot cuts and kills the growing point when the plant is in the seedling stage), yet no source of good resistance is known; the most resistance lines are badly damaged at times. While it is important to increase the gene frequency for resistance in desired lines and to identify the modes of inheritance in different sources of resistance, it is also desirable to improve the resistance of source varieties.

Some practical compromise is desired between agronomic suitability and degree of resistance. An effort should be made to simultaneously increase the gene frequency for resistance in agronomically good types and in source material. In due course, new composites involving better source material might be made. (Some breeders try to select new lines for resistance to shoot fly from single crosses; however, the F_1 and subsequent generations are as susceptible as the susceptible parent.) A certain amount of sorghum's inheritance for resistance is due to additive genetic variance, and some progress has been made by crossing and pedigree-type breeding.

It may also be possible to identify different components or mechanisms of resistance and to strengthen the level of resistance for each component separately. These might then be pooled together. Resistance to shoot fly has three major components: antibiosis, recovery resistance (the main stem is killed but a crop is made from the tillers), and oviposition nonpreference. High silica content in cells in the outer layers of the stem and lignin content are factors suspected to contribute to antibiosis. Trichomes (microscopic hairs on the under surface of the leaf) contribute to oviposition nonpreference. The presence of trichomes is controlled by a single recessive gene. Identification of various factors contributing to resistance (components of a quantitatively inherited trait) and the determination of their modes of inheritance may be important aspects in a program of breeding for resistance.

Intensity of Selection

The intensity of selection pressure can have significant effects. Natural infection is usually not as good

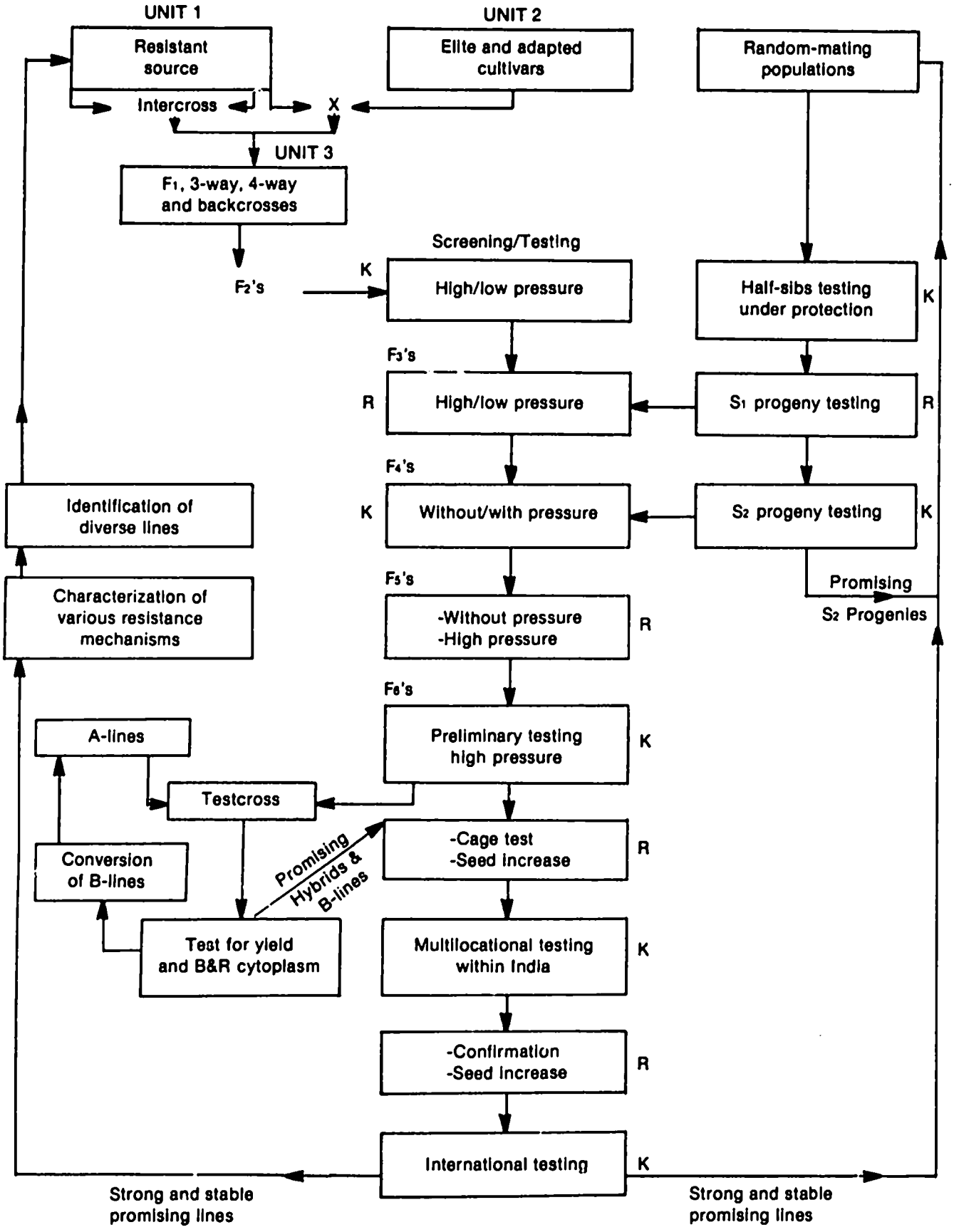


Figure 4.4: A scheme for pest resistance breeding in sorghum.

as artificially created epidemic or epiphytotic. The ability to control the severity of an epidemic or epiphytotic may be very useful; experimental work to develop screening techniques is very worthwhile for important disease and insect problems. Screening techniques for many of the important insect and disease problems of sorghum already exist.

Any method that could be used to gain reasonable control of the severity of an epidemic or epiphytotic would be of value when selecting breeding material. If the epidemic or epiphytotic is too severe, all plants may be affected and the selection differential lost. It is important to create a level of severity that results in a differential enabling useful selections to be made.

Environmental Factors

Environment affects the expression of many traits. Some diseases are more severe if the weather is cool and moist than if it is warm and/or dry. Some insects and diseases are more severe during one period of the year than during another. Attempting to achieve good expression of insect damage, or of a disease, in a climate not conducive to the insect or disease may result in an expression so poor that selection is not effective. Selection may have to be confined to certain seasons and/or locations. It may be possible to travel from one area to another in different seasons of the year; for example, selection for resistance to shoot fly would be possible in northern India (around 28°N) during the summer (March sowing) season and at Hyderabad (18°N) later in the rainy season (late July-August sowing). It also may be possible to mist water onto plants to increase the severity of grain molds, for example. The use of susceptible spreader varieties has been beneficial in screening pearl millet for resistance to downy mildew and sorghum to shoot fly.

At ICRISAT, different locations and sowing dates have been identified within India to help obtain the desired opportunity to screen for a particular disease, insect, weed, or environmental stress trait. The situation is something like this:

Moisture	ICRISAT Center (Oct, April) Anantapur (mid-May)
Stand establishment	ICRISAT Center and Hissar (mid-late April)
Shoot fly	ICRISAT Center (Nov-Dec) Hissar (mid-March)
Stem borer	ICRISAT Center (Nov) Hissar (July)
Midge	ICRISAT Center (late July) Dharwar (July)
Grain mold	ICRISAT Center (early June) Bhavanisagar (early June)
Downy mildew	Dharwar (late June, early July)
Charcoal rot	ICRISAT Center (Sept) Dharwar (Sept)
Rust	Dharwar (early July)
Anthracnose	Pantnagar (July)
Sooty Stripe	Udaipur (July)
Striga	ICRISAT Center (mid-late June) Akola (early July) Bijapur (Oct)

It can be appreciated that, in India, locations and sowing dates useful to evaluation of a particular problem trait have been found. Similarly, such an opportunity can be developed by any national program.

Breeding for insect and disease resistance involves an understanding of the genetic system involved and the manipulation of this system to make it better and/or to incorporate it into agronomically good varieties. The speed with which this can be done depends partly on how well the conditions can be controlled to make selection effective. It is important that scientists in the different disciplines involved work closely together and generally on the same varietal material.

Screening Procedures

A study has been made at ICRISAT to identify priority yield-limiting factors. Studies have been undertaken to develop screening techniques to enable routine evaluation of lines in the crop improvement program. Techniques for some traits are much easier to develop than for others. Techniques useful to screen for different yield-limiting traits tend to be unique, requiring a knowledge of the pest biology and ecology. Some of the procedures developed at ICRISAT are presented below.

Insect Resistance

A generalized breeding scheme for insect resistance is presented in Figure 4.4. The scheme is broadbased, involving pedigree breeding to strengthen the sources of resistance, to improve the agronomic quality of the source material, and to incorporate resistance into agronomically elite lines. It also includes a population breeding component relevant to accummulating genes for resistance from many possible sources. There are variations on this generalized scheme. Screening procedures for several insect pests are discussed below:

Shoot Fly

The shoot fly (*Atherigona soccata*) lays eggs singly on the undersurface of sorghum leaves of 5- to 20-day seedlings. The maggot hatches and migrates to the growing point and kills it, resulting in the drying of the central leaf, which is then called a *deadheart*. The shoot fly population can be monitored by using traps baited with fishmeal. In southern India the fly population increases in July, with peak periods in August and December. In northern India, there is a peak in March. Screening for resistance is undertaken in the field. Interlards of a highly susceptible cultivar are sown (four rows wide) as the fly population increases. Fishmeal is usually spread on the ground between rows of the interlards. After about 3 weeks—the time required to complete one life cycle—the test material is sown, usually 24 rows between interlards. Flies bred on the interlards attack the test material, which is in the susceptible stage. It is best to place a plastic label beside all seedlings with eggs, but no deadhearts, to assist in the selection of resistant plants at the time of harvest. Some varieties tiller after the main stem is killed and produce a crop; this is known as *recovery resistance*. Varieties found to have resistance are evaluated in cages where the female fly has no choice between varieties on which to lay eggs (to avoid oviposition preference). This test provides information relative to an antibiosis mechanism of resistance. Several mechanisms of resistance can be identified and varieties can be selected for antibiosis, oviposition nonpreference, and recovery resistance. It has been found that a simple recessive gene for the glossy trait (a glossy plant is usually light green and has a shiny leaf surface when viewed in the sun) contributes to shoot fly resistance. Seedling vigor is also important; any factor that slows down the rate of seedling growth usually results in greater damage by the shoot fly.

Stem Borer

Stem borers (*Chilo partellus*) attack the plant from the seedling stage (20 days old) to maturity. They can cause leaf damage, deadhearts, stem tunnelling, and peduncle breakage (generally accompanied by seeds of reduced size).

Resistance to stem borer can be evaluated at ICRISAT Center in a mid-June, October, or January sowing at uniform levels of infestation. In all cases, artificial infestation is required since the natural population is not high enough. The plants are infested when they are 15 to 20 days old (the best time should be determined according to location and season). Screening can also be done at Hissar in northern India where sowing is undertaken during July when the natural population levels are very high.

Artificial infestation is done by first using instar larvae from the rearing laboratory. The larvae are placed into a carrier and dropped into the whorls of test plants using a dispenser developed at CIMMYT (Fig. 4.5). Test plants are scored for the different types of damage caused, i.e., leaf feeding, deadhearts, stem tunnelling, and peduncle damage. Percentage of deadhearts in the seedling stage and peduncle damage as the head matures have been found to be the greatest reducers of grain yields.

Midge

Midge (*Contarinia sorghicola*) is a small (about 2 mm) bright orange-red fly that lays eggs in florets at the time of flowering. The maggot feeds on and destroys the developing seed.

It is difficult to realize a consistent and uniform population of midge in a screening field. They may

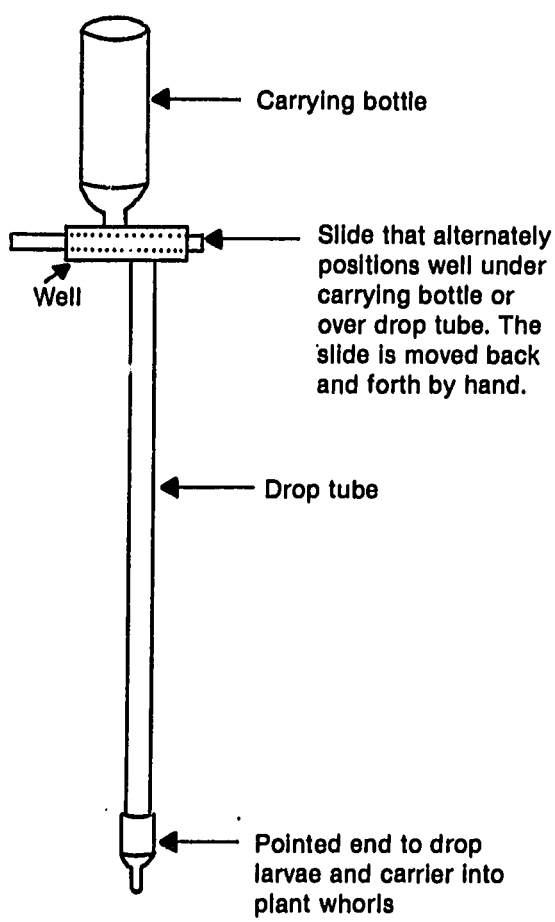


Figure 4.5: Larvae dispenser.

not occur every year, and the population can vary within the time span of flowering of the test material. It is therefore valuable to find locations and sowing dates at which the midge appears consistently. Use of more than one location will help insure that at least one location will have a good infestation.

It has not been possible to rear the midge on an artificial diet, but diapausing flies can be carried from one season to the next in infested heads. The midge population can be increased in the field by scattering infested heads from the previous season between rows of spreader and test material. There should be enough moisture, either from rain or from sprinkler irrigation, to realize the optimum number of flies. In India, ICRISAT midge-resistance screening nurseries are sown in late July-early August at ICRISAT Center (Patancheru) and at Dharwar. First, spreaders of mixed maturity are sown, and after about 2 weeks (midge has an 11-day life cycle), the test material is sown. It is useful to sow a susceptible variety after every 15 to 20 rows of test material to evaluate uniformity of attack; however, the population of midge may tend to be high around the check rows and migrate more into neighboring rows, causing more damage than if the entries were sown away from the check. The number of check rows should be only enough to monitor the uniformity of infestation. Using two sowing dates about 15 days apart helps ensure that test entries of all flowering dates are subject to midge attack.

The resistance of varieties selected from such a field screen can be verified with a head cage (Fig. 4.6). A wire frame is made about 16 cm in diameter and 25 cm in length. The wire frame is covered with blue fine cloth mesh (because midge are not attracted by blue, they spend more time on the sorghum head). Midge flies are caught in the morning. A vacuum sucking aspirator can be used, and the suction can be provided by the mouth or a machine. A total of 80 flies, 40 on each of 2 consecutive days, are released in each cage. (Midge flies live only 1 day.) Susceptible checks should be included in the test. Percent seed set can be recorded to indicate the level of resistance. Varieties with adequate levels of resistance have been identified.

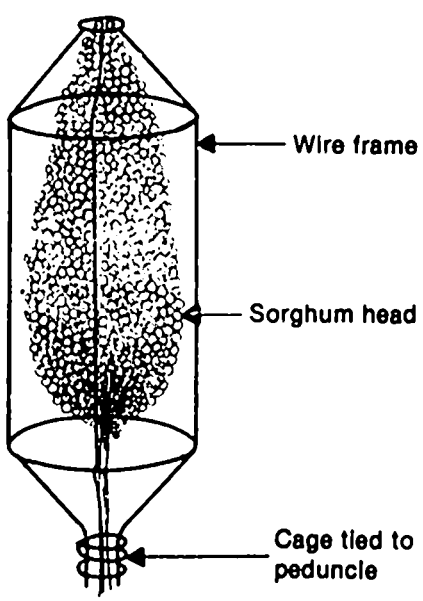


Figure 4.6: Head cage for midge.

There have been difficulties in India with high head bug populations in the midge-resistance screening nursery. The head bugs suck juice from developing seed, but they also kill the midge maggots. A spray of carbaryl just after postanthesis has been found to greatly reduce the head bug population but not the midge eggs or maggots within the florets.

Diseases

Downy Mildew

Location is important in screening for downy mildew. ICRISAT has been much more successful in screening for resistance at Dharwar than at ICRISAT Center near Hyderabad. The climate at Dharwar is a bit cooler, and during the growing season light rains are common several times a day.

An infector-row technique, based on windborne conidia of the SDM pathogen (see ICRISAT 1981 Annual Report), has been successfully used to screen more than 4000 sorghum lines for SDM resistance during one rainy season at Dharwar. The components and procedures of the technique follow:

1. Sow in infector rows a highly SDM-susceptible sorghum line (DMS-652 or IS-643) on which the pathogen produces abundant conidia.
2. Establish SDM disease in infector rows by incubating germinated (24 hr) seeds between SDM systemically infected leaf pieces at 20°C in a dark, humid chamber for 18 to 20 hr before sowing to ensure that all infector-row plants are infected.
3. Plant the test material after infector-row seedlings have become established and show sporulation of SDM at about 20 to 25 days after sowing.
4. Plant four rows of test material between two rows of infector rows.
5. Evaluate the test material for SDM at seedling, flowering, and maturity stages, considering material with 5% infected plants as resistant.

Downy mildew development and conidial production in the infector rows has been high; there has been 100% systemic disease in check rows, indicating adequate disease pressure for evaluating test material.

Of 2804 germplasm and 1126 breeding lines screened, 151 and 334 lines, respectively, were resistant to SDM; 44 were free from the disease.

Resistance of field screened plants can be confirmed by germinating test material folded in a leaf adjacent to the white down formation of the disease. The folded leaf should be kept in an incubator at 18-20° C and 90-100% relative humidity. Sorghum is most susceptible to the disease in the seedling stage, and this folded leaf technique is a severe test for resistance.

Grain Mold

The two grain mold fungi of primary concern at ICRISAT are species of *Curvularia* and *Fusarium*. There is also a lower priority concern for resistance to *Phoma sorghina*. The screening nursery should be sown when rains and high humidity are expected during the grain-filling and maturation stage. Availability of sprinkler irrigation is valuable, as the screening nursery can be watered periodically for about 1 hour on rainfree days. Initially, at 50% flowering stage, the heads should be sprayed with a mixture of *Curvularia* and *Fusarium* spores. After spraying, the heads should be bagged using regular paper pollinating bags. Subsequently, adequate levels of grain molding for good screening purposes can be realized without inoculation or head bagging as long as sprinkler or mist-type irrigation is available. However, for special studies on grain molding, inoculation and head bagging should be done. Expression of head mold is maturity-related, so it is important to note the days to 50% flowering of all entries in the screening nursery. If possible, lines of the same maturity should be grouped together in the screening field. Scoring is undertaken about 55 days after flowering. A 1 to 5 score is used where 1 = no mold, 2 = 1 to 10% grains of a panicle molded, 3 = 11 to 25% grains molded, 4 = 26 to 50% grains molded, and 5 = more than 50% grains severely molded. If a 0 to 9 score is used, the odd-numbered score would be essentially equivalent to scores of 1, 2, 3, 4, and 5. Recently a number of entries that are virtually immune to grain molding and other forms of weathering have been identified in the world collection. While all of these have colored grain, they do not all have a testa or high tannin content. Seeds of these varieties are available from ICRISAT.

Leaf Rust and Anthracnose

The causal fungi of rust and anthracnose are *Puccinia purpurea* Cooke and *Colletotrichum graminicola* (Cesati) Wilson, respectively. Rust is favored by cool (18-25° C) and moist conditions, whereas anthracnose is more prevalent in warm (25-30° C) and humid areas with high rainfall. At ICRISAT the methodology for evaluating lines involves screening with an infector-row technique at hotspot locations (Dharwar in southern India for rust and Pantnagar in northern India for anthracnose) where favorable environmental conditions and abundance of inoculum sources support severe disease on susceptible lines. (The screening nursery should be sown at such time that the susceptible stages of the crop—at and after flowering—coincide with a favorable environment for disease development.) In the infector-row technique, test rows (five for anthracnose and seven for rust screening) are sown between two infector rows of highly susceptible sorghum lines sown at least 2 weeks earlier. The infector rows may be inoculated by placing infected plant debris in the whorls of 30- to 40-day-old plants. The middle row of the test entries (third for anthracnose and fourth for rust) is sown to the same variety as the infector row to serve as a check and indicator of disease pressure. At the soft dough stage, disease severity (as measured by the percent leaf area damaged of the top four leaves) is recorded on a 1 to 5 rating scale where 1 = no disease, 2 = 1 to 5% leaf area damaged, 3 = 6 to 20% leaf area damaged, 4 = 20 to 40% leaf area damaged, and 5 = severe disease with more than 40% leaf area damaged. At ICRISAT many sorghum lines have been identified that have high yield potential and resistance to either anthracnose or rust, or to both.

Striga

Striga is a parasitic weed attacking sorghum in much of Africa and on the Indian subcontinent. It is also a problem in a restricted area of North Carolina in the USA.

Screening for *Striga* resistance is difficult; the weed pest may not appear every year, and it never is uniformly distributed in a screening field, even when artificially infested to make a sick field. A *Striga* sick nursery should be sown on well-drained fields of reasonably low fertility. High input of nitrogen fertilizer is not desired, but the nutritional base of a sick field must be adequate for good development of sorghum plants. Deep plowing is not as desirable as seedbed preparation measures that

work only a shallow soil surface (5 cm or so). Mechanical cultivation should be completed early so as not to damage the *Striga* plants that will be emerging about 30 days after sorghum emerges.

Sowing a screening nursery in *Striga*-infested fields at several different locations in a country will help ensure that good expression of the weed is realized in at least some locations each year.

A three-stage testing procedure has been developed to evaluate lines and varieties for resistance. Each stage involves an increasing association of test material with a susceptible check. A comparison of the resistance of the test material is always made with the nearest check rows. Test material is always evaluated from stage 1 through stage 3, ending up in the most resistant types. The first stage of testing is in an unreplicated trial of a large number of entries with two rows per entry. A susceptible check is repeated after every four test entries. The entries advanced from stage 1 are tested at several locations in three row plots and replicated at least three times. Checks are systematically arranged in such a way that every test entry plot will have one check plot adjacent to it (Fig. 4.7). All comparisons in stage 2 are restricted to the small area consisting of eight test entries with a check plot in the center. In stage 3, selected entries from stage 2 are tested in five-row plots and are arranged so that every test entry plot is bordered by susceptible check plots on its four sides, giving the field a checkerboard appearance (thus the name *checkerboard* layout). The layout provides a useful opportunity to estimate grain yield from replicated test entry plots in *Striga*-sick fields and, at the same time, monitor the numbers of *Striga* plants on each test entry and the adjacent susceptible checks, thus providing a good estimate of the resistance of the test entry. It is necessary to count the *Striga* stand in a measured area of all plots several times during the season (one flush of the weed can come and go, and another flush comes). A statistical procedure has been developed at ICRISAT to analyze these data. Using this three-stage testing procedure, breeding lines with a very high level of field resistance have been developed.

Stand Establishment

Stand establishment is defined as germination, emergence through the soil surface, and early seedling growth. Techniques have been developed to evaluate emergence through a soil crust and through a hot soil surface to measure seedling drought resistance and to score for seedling vigor.

Soils differ and the technique to create a uniformly crusted soil may vary. An Alfisol with relatively high sand content (55% course sand, 23% fine sand, 5% silt, and 7% clay) is used at ICRISAT. The field should be thoroughly prepared so that there are no weeds, raised beds 150 cm wide are formed and shaped with a bed shaper, leaving a smooth flat

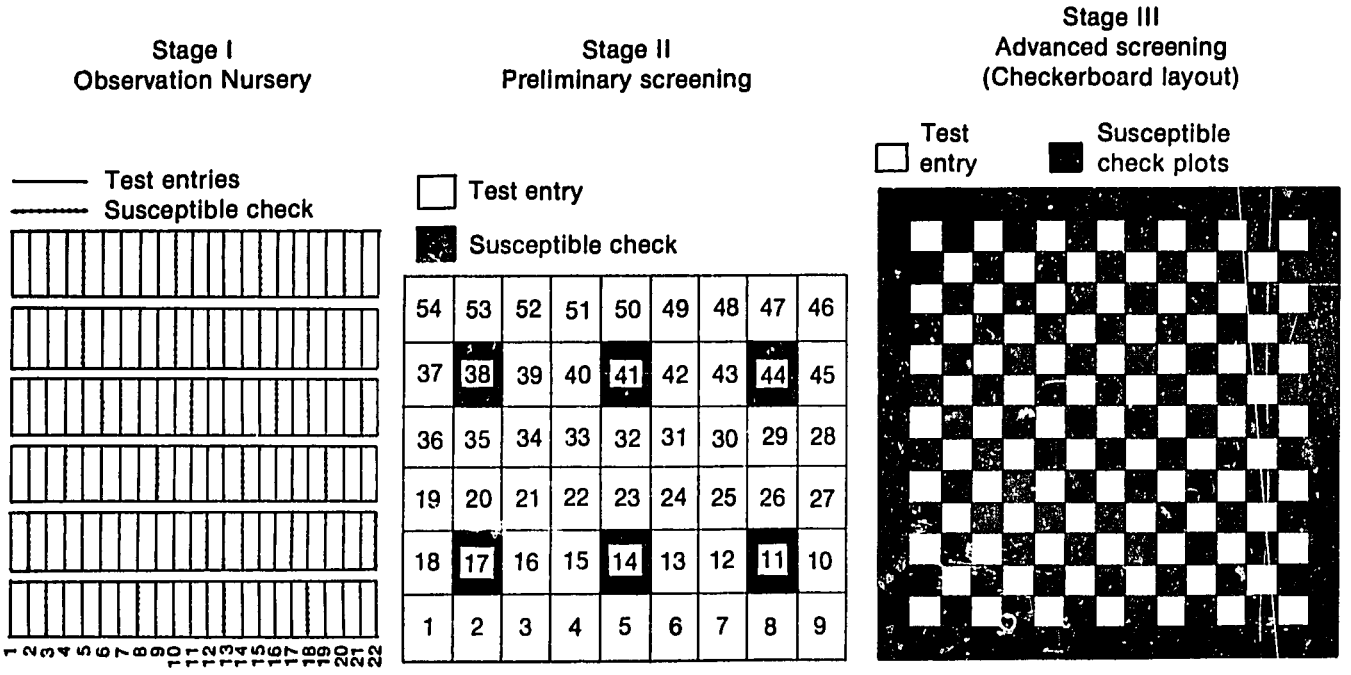


Figure 4.7: A three-stage screening method for *Striga* resistance in sorghum.

top of about 130 cm, and the field is sprinkler-irrigated to provide moisture for germination. Four rows are sown across the bed, care being taken that the counted number of seeds are all sown at the same depth. Sprinkler irrigation lines are placed so that each line will wet 10 beds. After application of 35 cm of water, the surface is allowed to dry and crust and the crust is mechanically broken over the center of one row of the two-row plot. This permits a direct comparison between emergence through a crust and emergence in the absence of a crust. Checks are also interspread in the test field to evaluate the uniformity of the crust formed. Evaluation is undertaken at a time of year when rainfall is not expected; otherwise it should be done under a rainout shelter. This procedure is very uniform and repeatable, with CVs of less than 10% being realized. Better entries thus far tested have an emergence of 60% of the no-crust treatment; in many cases emergence is zero.

Emergence Through a Hot Soil Surface

Large brick, plastic-lined flats (containers) 100 x 150 x 20 cm are constructed on a raised soil pad on the ground to permit drainage. Some 20 entries are sown in short rows (45 cm) at a uniform depth of 3 cm, providing two replications per flat. The soil is made just wet enough to permit germination and emergence. Three flats are sown in an identical fashion, except that entries are randomized. In one flat the soil surface is covered with charcoal, and soil temperatures rise above 60° C; another is made white by spreading Kaolin and temperatures remain in the low 40s; the third flat, with red soil and temperatures in the upper 40s, is untreated. The test is conducted during the hot, dry time of the year when daily maximum air temperatures range from 38° C to 42° C. When emergence through a hot soil surface is measured in this way, moisture availability and soil temperature are confounded.

In some places emergence through a cold soil surface is of concern. A similar procedure may be possible by sowing in early spring months when air temperatures are above freezing and soil temperatures low.

Another technique has been developed where test plants are sown in 15-cm pots; the pots are placed in a tray containing water to a depth of 10 cm; and a bank of infrared lights is mounted above the pots so that the height of the bank of lights can be changed. The desired temperature of the soil can be obtained by adjusting the distance between soil surface and lights. The soil is kept constantly moist by capillary action of water from the tray, assuring that temperature effects are not confounded by soil moisture availability.

Seedling Drought Resistance

Brick flats as described above are used, sowings are made in the same way, and only enough water is provided for germination and emergence. The seedlings are allowed to wilt, and a score is taken periodically throughout the process. When more than 50% of the test entries have permanently wilted, the flat is rewatered and recovery is scored after 4 hours and 24 hours. The same test can be conducted with greater precision in the greenhouse using pvc tubes 10 cm in diameter and 30 cm deep. About 12 seeds are sown in a circle in the tube and after emergence thinned to 8. Scoring is done as above, with 1 being used for least wilting and best recovery and 5 being poor for the traits. Some tubes must be sown with standard check varieties. A glossy trait found in sorghum has been found to contribute to seedling drought resistance (Tarumoto et al. 1981).

Seedling Vigor

A study was made to evaluate different methods to test for seedling vigor. Correlation of visual scoring with other methods was good, and visual scoring on the basis of 1 = good to 5 = poor is recommended. Scoring can be undertaken some 10 to 20 days after emergence. As one begins to score he will gain a "feel" and be able to assign scores with confidence (Maiti et al. 1981).

It is important in all of these studies that great care is taken in selection of the seed used. Seed should be carefully graded so that all are sound, plump, and of normal size. They should be from good storage, and storage time should be of about the same duration. Ideally, seed used should come from the same field-grown crop of test entries. If this factor is not carefully controlled, some of the differences observed could relate to the seed used rather than to a varietal characteristic.

Breeding for Food Quality

Sorghum is grown in the semi-arid tropics (SAT) mostly as a food crop in the rainy season. Traditionally, farmers select plant types that flower at the end of the rains, so that the grains ripen bright and clean in dry weather and have excellent food quality. Consistency of yield and quality are more important than quantity. On the other hand, varieties of recent

origin have been selected for earliness, improved harvest index, higher productivity, and most important of all, stability of yield across normal and abnormal years. However, such photoperiod-insensitive, high-yielding genotypes often mature in wet weather and pose a host of grain quality problems. Use of exotic germplasm also frequently leads to unforeseen consumer quality problems unless acceptable grain types are identified and selected in the early generations of a breeding program.

Grain molds and weathering are the most important factors affecting the grain quality of the rainy-season crop. Moldy and weathered grain may not be usable or will make a very inferior food. Problems created by humid and wet weather are: susceptibility to parasitic and saprophytic fungi that destroy the grain; pigmentation and grain weathering; and loss of seed viability and/or sprouting.

Since farmers' preferences depend upon the consumption value of the grain and its market price, grain deterioration and inherent food quality problems become crucial for the extension of high-yielding genotypes.

A close association exists between grain-weathering and molding problems and those of food quality. As they are interrelated, aspects of both are considered in this section.

Grain Molds

Etiological studies have shown that saprophytic as well as parasitic fungi cause grains to mold and that these organisms attack the grain in the early stages of development. Hot and humid environments favor their growth. Seventeen fungal species belonging to eleven genera have been isolated from molded grain at ICRISAT Center. The most important parasitic molds are species of *Curvularia, Fusarium, Phoma, Olpitrichum*, and *Trichothecium*. Most work has been done on *Curvularia*, which turns the seed a sooty black, and *Fusarium*, which turns the seed pink.

Breeding for host plant resistance is probably the most practical solution to the grain mold problem. A screening technique has been standardized (see subsection on Grain Mold, above)

A breeding program to utilize sources resistant to grain molds is outlined in Figure 4.8. High-yielding and good grain parents from various sources were selected and appropriate crosses were made in single, double, and three-way combinations. Selection in the F_2 was under natural conditions, but from the F_3/F_4 generation onwards families were inoculated with *Curvularia* and *Fusarium* spp to identify those that were less susceptible.

It is important to protect entries in the mold screening nursery from head bugs. Damage by these insects will interfere with mold ratings. Control is possible by spraying or dusting carbaryl (Sevin) just after flowering. It may be necessary to spray or dust several times because of variable maturity of entries being evaluated.

The process of selection followed by testing is a continuous process, and as better levels of resistance become available in more agronomically superior and more genetically diverse backgrounds and with good food quality traits, poor and less diverse material is rejected. Development of an array of genetically diverse lines with good food quality and mold resistance in diverse varietal material is an important objective (Murty et al. 1980).

Evaluation of Food Quality

There are two fundamental concepts in evaluating sorghum for food. Useful and repeatable screening procedures must be developed, and the research needs to be undertaken in cooperation with people who normally eat a particular preparation and can tell if a sample is good or bad.

Basic Food Types Made from Sorghum

There are many ways in which sorghum is prepared as food, but they can be classified into nine groups for food evaluation purposes:

1. Unleavened bread (roti - India).
2. Leavened bread (injera - Ethiopia; kisra - Sudan).
3. Bread from alkali cooked grain (tortilla - Mexico and Central America).
4. Stiff porridge (ugali - eastern Africa; tô, teau - West Africa; bogobe - Botswana; sangati - India).
5. Thin porridge (ugi - eastern Africa; edi, ogi - Nigeria; ambali - India).
6. Boiled grain (whole or broken - China, India, scattered in Africa).
7. Pasta products (noodles - China).
8. Beverages (wine - China; beer - Africa; soft drinks - Africa, Latin America).
9. Snacks (pop and sweet sorghum).

Grain Traits Affecting Food Quality and Acceptance

Grain Color: Grain used to make food is predominantly white. However, in regions like East Africa where sorghums are traditionally grown to avoid bird problems, brown grains are acceptable. These colored grain types may or may not have a high

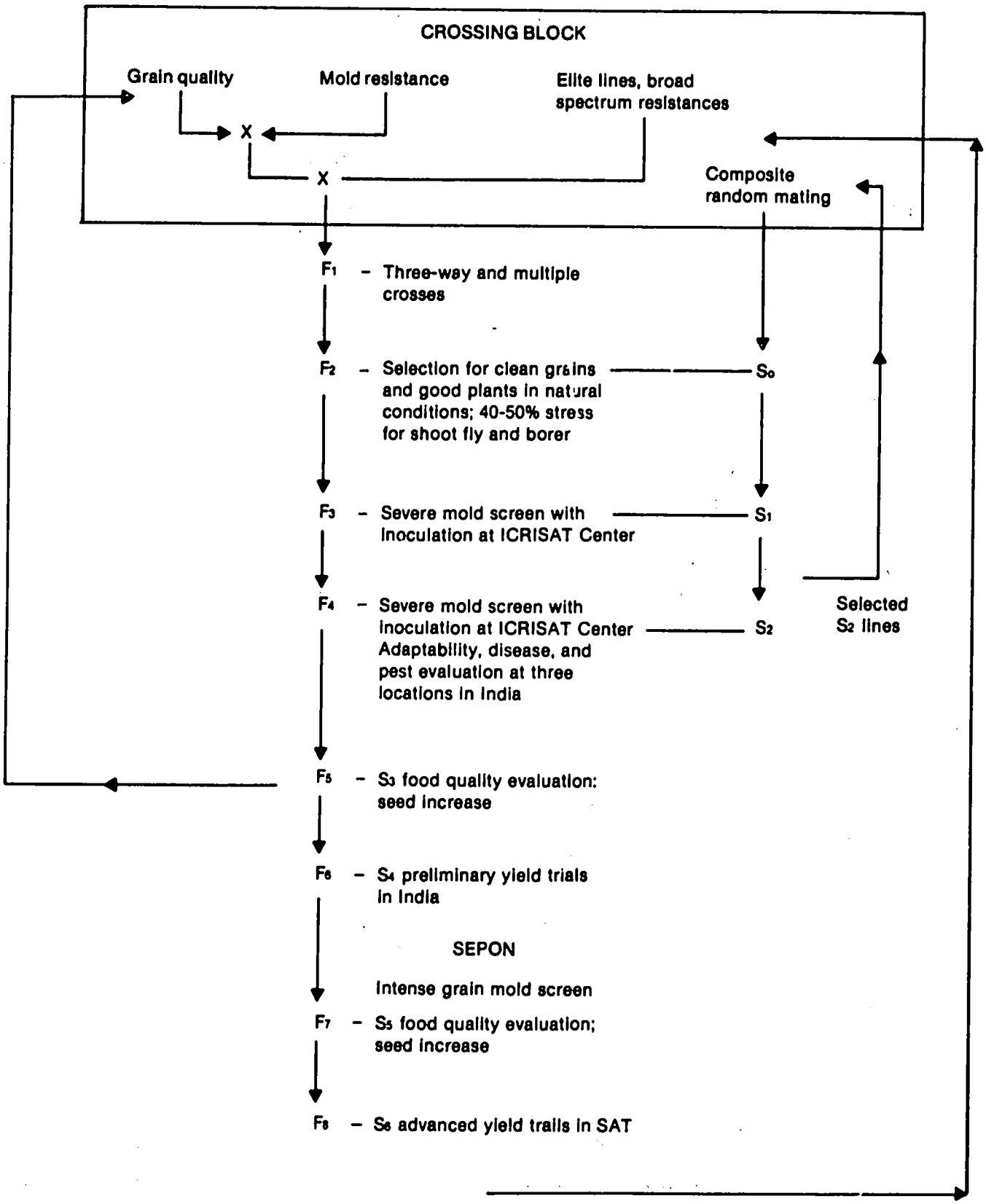


Figure 4.8: A scheme for breeding improved grain quality and mold resistance.

concentration of tannin. Tannins are chemically high-molecular-weight, soluble polyphenols, which inhibit protein digestibility, and thus high tannin types are of low value even for feed purposes. The red grain types, free from tannins, have been found to be particularly suitable for brewing. Dehulled red grains can also give attractive food products.

It is visually difficult to assess the tannin content in sorghum. White- and red-pericarp types free from subcoat have no/or negligible tannin content. Thus only brown (including white grains with subcoat) grains require evaluation for tannin content when food quality tests are conducted.

There are some regions where brown grains are used for food consumption; however, such grains are usually not preferred. Acceptability of any food depends on the options available to the consumer. Therefore, scientists should look for and select what is desirable in the environment in which the crop will be grown. White grains are the most widely accepted. It is worthwhile to evaluate them in areas using color-seeded types. Since grain color is controlled by major genes (see Section 3), it should be reasonably easy to combine white grain color with other agronomic characters. There is no evidence that white grains lead to reduced diversity for other traits (polygenic variation in general) or vice versa.

Grain Size and Weight: Generally bold grains are preferred. Grain size and grain weight are positively correlated. A hundred-grain weight of 3.0 to 3.5 is acceptable. Increased grain weight/100 seeds is generally correlated with soft endosperm and susceptibility to grain molds and storage pests. Frequently boldness of the grain is visually judged, but evaluations should be supported by grain weight measurements of at least those entries present in yield trials.

Grain Shape: Round or oval grains are preferred. Round and oval grains have processing advantages in the traditional as well as mechanical milling methods. It is more difficult to remove the pericarp of beaked and flat grain types. Unfortunately beaked and flat types are dominant. Selection should be for round or oval types.

Pericarp: A thin pericarp (dominant) is generally preferred. In several African countries a thick pericarp, coupled with hard endosperm, is advantageous for traditional dehulling (pearling). In the Indian subcontinent, however, thick pericarp types are disliked. So both thin and thick pericarp types are useful. It is important to keep these factors in mind in selecting lines for testing in various countries.

Plant Color: Grains from tan plants show the least spotting on the grain. Even among the tan plants there is some variation in the intensity of plant color, so grains of these plants also require visual examination for absence of yellow tinge, spots, etc. Selection for the lightest color is preferred. Selection for tan plants is only to avoid pigmentation on the grain. Dew or rain during maturity is enough to cause colored spotting on the grain borne by red and purple plants. Insect bites and other injuries also result in colored spotting. Glumes should be straw or sienna colored. Color from the glumes often leaves spots or a tinge on the grain.

In dry regions, where maturity and rainfall do not coincide, purple and red plants can more readily be used. Selection for tan plants should not lead to restricted diversity; however, it may be useful to maintain good red and purple germplasm with desired traits in crossing programs. Plant color is governed by major genes and can be recombined with any other character.

Endosperm Characters: Waxy grains should generally be avoided, as there is no preference for them in any country except China. In fact, waxy grains lead to several food quality problems. Because they are not easy to detect in the field, it is useful to identify waxy varieties while beginning the crossing program and manage crosses with waxy parents separately if the trait is wanted. Waxy endosperm is controlled by a single recessive gene; the starchy endosperm exhibits xenia.

There is limited preference for yellow endosperm, but this is not critical. Inheritance of yellow endosperm is not completely understood, but it is known to be controlled by a few genes. The yellow-endosperm grains have disadvantages: they are highly susceptible to grain deterioration and also to storage pests. The carotene, of low vitamin A activity, is lost in storage and even through exposure in the field. Viability of seed after storage can also be limited. Therefore yellow endosperm-types should be selected only for use in drier regions. White-endosperm types are generally preferred.

Texture: This trait relates to the proportion of flower versus corneous endosperm in the kernel and is the most important factor governing food product quality. It can be visually evaluated by cutting a few grains and observing the proportion of vitreous endosperm. Generally the more vitreous the endosperm the harder the grain. Floury endosperm renders the grain soft. Good quality thick porridges popularly consumed in African countries can be obtained from hard grains. Intermediate-to-soft endosperm types are good for leavened breads con-

sumed in Sudan and Ethiopia. Roti, tortilla, and boiled rice-like products prepared from grains with intermediate texture show good quality.

Hard and dense endosperm appears to dominate over soft endosperm, but this observation requires further detailed studies.

Experience suggests that grains with "exposed" embryos such as those seen in many caudatum types germinate on the panicle more frequently than grains with deep-seated embryos.

Selection for Food Quality Traits

Selection for the plant color and pericarp color and thickness factors should be carried out in the F_2 and F_3 generations. Since these factors are more or less fixed by this time, further scope of selection is poor. Grain size and shape, grain weight, and endosperm texture should be selected in F_2, F_3, and F_4 generations. Progress of selection within families for these characters is also poor beyond the F_4 generation.

Further evaluation of the suitability of the field-selected material for any food product can be done only in a laboratory. Current knowledge indicates that we can exercise only about 50 to 60% confidence in the food quality of field selections.

Methods Used for Roti (Chapati) Evaluation

At ICRISAT, the most work on food quality evaluation in sorghum has been for making roti (an unleavened bread); therefore, it will be used to illustrate the nature of the research problem.

The quick tests used to evaluate food quality in wheat are not suitable for sorghum; such a technology needs to be developed. A search for quick tests is still in progress. Initially, an effort was made to standardize the steps in making roti. Tests developed are as follows:

Grain: Color, weight, density, endosperm texture score. Endosperm texture is determined on a scale of 1 to 5 (1 = 0-20% floury to 5 = 81-100% floury), by breaking strength (kg), and by percent water absorption of the grain after soaking in water for 5 hours at room temperature.

Flour: Flour particle size index (PSI). PSI is a relative measure of average particle size of a flour sample. It can be determined as the percent of a flour sample passing through a standard sieve (for example 75 μ).

Dough: Water required (mls) to make dough from 30g flour, kneading quality score (1 to 3), rolling quality (diameter in cm.).

Roti: This food is tested for color, taste, texture, aroma, and keeping quality as follows—

- color - grain, dough, and roti colors are compared with the Munsell soil color charts;
- taste - 1 good to 5 bad based on taste panel evaluation;
- texture - 1 very soft to 5 very hard;
- aroma - 1 pleasant to 3 unpleasant;
- keeping quality - 1 good to 5 very bad.

Taste, texture, and aroma were determined by a taste panel whose members were selected because they were traditional consumers and could consistently evaluate these traits in different samples.

Genetic Variation: A selected set of 422 genotypes of diverse origin and grain color were evaluated in replicated observations. These 422 genotypes reflected a broad range of variation, except for grain density. Physical characters of the grain-endosperm texture, breaking strength, and percent water absorption had broad variation. The dough quality characters—water required for dough, kneeding quality score, and rolling quality—had a moderate variation. The range of organoleptic quality scores was also wide, and varied from 1 to 5. It is apparent that the variation for grain quality parameters is great, enabling selection for different food types to be effective.

A subset of 167 entries from within the 422 with white, creamy white, and pale yellow grain varied as much as for the whole set. This observation reflects the difficulty in selecting for good food quality grains based on visual attractiveness (Table 4.19) (Murty et al. 1982).

Selection Criteria for Roti Quality

Variation from year to year has been found highly significant for 100-grain weight, breaking strength, percentage water absorption, dough-kneading and rolling quality, chapati aroma, and keeping quality; similarly genotype x year interaction was highly significant for several characters. This emphasizes the importance in carefully selecting conditions for growing plants for food quality evaluation. It is best to make comparisons between varieties grown in the same field in the same nursery. If variability is high year to year then environment has a strong influence on the trait.

Breeders can select in the early generations for white and yellow (endosperm) grains, free from subcoat and with a thin pericarp and 60 to 70% corneous endosperm. Grain samples from F_3 and F_4

Table 4.19: Variability for grain, dough, and roti quality attributes among 422 genotypes of sorghum.

Attribute	Mean + SE	Range	
		Maximum	Minimum
Grain			
Endosperm texture	2.5 + 0.03	5.0	1.0
	(2.5 + 0.05)*	(4.0)	(1.0)
Grain weight (g/100)	3.49 + 0.043	7.63	2.04
	(3.43 + 0.048)	(5.27)	(2.04)
Breaking strength (kg)	8.4 + 0.09	14.6	0.8
	(8.9 + 0.15)	(14.6)	(5.5)
Density	1.26 + 0.002	1.38	1.002
	(1.23 + 0.002)	(1.32)	(1.119)
Water absorption (%)	25.3 + 0.23	43.1	12.4
	(26.3 + 0.38)	(42.1)	(14.4)
Dough			
Water for dough (ml)	27.9 + 0.12	38.9	20.9
	(27.2 + 0.17)	(37.5)	(20.9)
Kneading quality	1.2 + 0.22	3.0	0.5
	(1.1 + 0.01)	(3.0)	(0.5)
Rolling quality (cm)	22.0 + 0.06	22.8	15.2
	(22.3 + 0.08)	(25.4)	(16.2)
Roti			
Taste	2.3 + 0.03	5.0	1.0
	(2.0 + 0.04)	(3.5)	(1.0)
Texture	2.2 + 0.02	4.5	1.0
	(2.2 + 0.04)	(4.0)	(1.0)
Aroma	1.4 + 0.02	3.0	1.0
	(1.4 + 0.03)	(3.0)	(1.0)
Keeping quality	2.8 + 0.03	5.0	1.0
	(2.6 + 0.04)	(4.5)	(1.0)

*Numbers in parentheses refer to the selected set of 167 entries.

material can be evaluated for desirable physical properties of grain, such as low water absorption. Flour and dough tests are best undertaken from the F_5 generation onwards, and laboratory taste panel evaluation of rotis can be done on elite F_6 material under yield tests. Consumer preference tests are necessary for only a few of the most advanced cultivars. This procedure represents a sequence from elimination based on visual inspection of the seed to selection based on laboratory tests, to the actual preparation of the product.

Environmental Factors Affecting Grain Quality

Moisture: Grains from the rainy-season crop frequently show reduced grain weight and breaking strength, increased water absorption, and relatively poorer organoleptic properties. These differences can be reduced by selecting in both rainy and postrainy seasons.

Ten samples were grown under stress and no-stress moisture treatments. Samples were cleaned so that only plump, sound grain was used from both treatments. Drop in yield because of stress was 38.5%. There were differences in endosperm texture, 100-grain weight, percent water absorption, water for dough, and rolling quality. However, these differences were statistically nonsignificant; changes in roti taste, texture, aroma, and keeping quality were also not significant. It would appear that moisture deficiency does not have a major impact on food quality as long as the grains are normally developed.

Location: Grain samples from two locations in India, Mohol and Bijapur, produced rotis that were superior in quality over those produced from the same variety (M35-1) at ICRISAT Center (Patancheru). In all cases the seeds were from the postrainy season.

Fertility: Six cultivars were grown with nitrogen applications of 0, 60, 120, and 200 kg/ha. Most differences were found between 0 and the other levels of N application, but they were not statistically affected by nitrogen application.

Clearly, rain and humidity at the time of grain development are the most important environmental factors affecting grain quality. Experience indicates that it is important in conducting tests for food quality to compare breeding stocks, that seeds are from entries grown in the same field and season.

Field Support Techniques

Crop Management

The selections made by a breeder are based on comparisons between entries. Thus nurseries and yield trials should be grown in uniform conditions that produce vigorous growth. No breeder can identify genetic potential if it is completely masked by a poor environment.

A breeder should select the most appropriate field for his work and then farm it so as to preserve uniformity. (This ideal is seldom achieved but should remain a goal.)

Conditions will vary considerably. In parts of the tropics the water supply is erratic, thus drainage—and possibly irrigation—is important. The fields selected should be drained adequately, or shaped so that there will be uniform flow of water onto and off them. Plant growth in low spots is favored in a drought and retarded in a period of high rainfall. Ridging and furrowing can be quite useful. Plants should be sown on the tops of the ridge (bed), unless there is a salt problem (if salt is a problem, plants might then be sown on the side of the bed off center, or in the center of a sloping bed). The bed should be broad and flat, rather than steep and narrow. If heavy rains come, steep narrow ridges usually erode and plants will lodge (especially young plants). Generally, land that is shaped for irrigation is also well shaped for drainage.

Precision in the farming operation is required for good breeding, as well as for good general farming. Rigidly fixed heavy equipment drawn by animals or tractor generally does a more precise job of moving soil than do light wooden implements, frequently drawn by animals, that tend to cut deep in wet areas and fail to penetrate dry hard land surfaces. Banded fertilizer may be closer to seed in one part of a row than in another part; shoes on a fertilizer applicator should be kept open, especially if the soil is moist. The use of tractor equipment presents problems, but usually does a better job.

When considering mechanization, a breeder should place as much emphasis on drivers, mechanics, and spare parts as on the equipment. If the full complement can be obtained, tractor equipment will facilitate quicker and better land preparation, cultivation, and plant protection. Thus, experimental areas can be larger, and in tropical areas land can be prepared rapidly enough that three generations a year can be obtained.

Nitrogen fertilizer should be used on the nursery and yield trial, whether moisture might be limiting or adequate. The rate of application should vary between 30 to 40 kg of N/ha in low moisture conditions, and 150 kg of N/ha if moisture is adequate. If rainfall is high, loss of nitrogen may occur due to leaching or denitrification, and more fertilizer should be added. The level of nitrogen should be sufficiently high that the plants do not suffer nitrogen stress. Nitrogen application should be split, one-half being banded near the seed (5-10 cm) at sowing, and the remainder applied about 35 days after emergence. Banding the fertilizer will help prevent fertilization of weeds and may aid rapid seedling growth in areas where shoot fly is a problem.

Phosphate and potash fertilizer should be applied to balance with the nitrogen used. Superphosphate can be broadcast and worked into the soil. Minor elements may be important (iron and zinc have been found to be important in India). An iron deficiency can be corrected by spraying a 3% solution of ferrous sulfate to wet. Zinc deficiency can be corrected by applying about 10 to 25 kg/ha of zinc sulfate with the fertilizer or by spraying an 0.5% solution to wet the plants. A small amount of detergent (approximately 10 cc/15 liters) should be used in the spray to lower surface tension to achieve better coverage.

Granular fertilizer should be used if it is applied with a mechanical planter. A marker that will indicate where the seed should be placed should be fastened to the fertilizer applicator. If the fertilizer is placed with locally made equipment or by hand, care should be taken that seed and fertilizer do not come into contact with one another. Frequently, good animal-drawn spreaders are available. Seed can be drilled or hill planted. A final population of 150000 plants/ha is sufficient to obtain good plant expression. If highly heterogeneous material or

segregating generations from a crossing program are grown, space-planting (75 cm between rows and 25 cm between plants) may be desirable, as plant expression can be observed with less influence of between-plant competition.

Repeated cropping of the same field with sorghum may not be advisable; it is especially important to germinate dropped seeds of the previous crop before resowing, or the problem created by volunteer plants can be severe. This can be done by pre-irrigating the field. There have been several cases in India where a nematode problem has become severe after three or four consecutive sorghum crops. Under such circumstances, crop rotation is recommended, preferably with a noncereal crop. Nematode damage has appeared in two forms: the plants in a field were primarily stunted, with randomly scattered or small groups of normal plants; or secondly, all plants in a sector of a field were stunted and outside the sector were normal. In one case, the host range of the nematode was fairly wide, affecting both sorghum and a subsequent legume crop. If nematocides are used for control, they frequently must be placed in the ground several weeks before sowing.

Protection from insect pests may be desirable in a nursery and probably also in yield trials. The only reason for not protecting the plant is to create a selection differential for resistance or to study some genetic problem involving the resistance. Several factors are important when considering the use of plant protection measures in a nursery. It may be that the pest is seasonal and that the nursery is being grown during the season when the insect is active to advance a breeding program aimed at releasing a variety in the season when the insect is not active. Protection may also be necessary while selecting, crossing, or otherwise including unadapted germplasm. It may be possible to dramatically increase yields with a susceptible variety. Pest control might be economical and feasible. The use of the pest control practice could then be part of the package of recommended practices. Breeding efforts to utilize available resistance should be undertaken as soon as sources are identified.

There are good insect predators of mites and aphids. Insecticides should not be used that might kill beneficial predators; these predators can often be more useful than the insecticides. For example, there are predatory mites and small beetles (1 to 2 mm) that are effective predators of the mite. The use of a sprayed insecticide to control stem borers may kill these predators and result in a severe mite attack. Granular insecticides are recommended for this situation. Aphids are frequently effectively controlled by the ladybird beetle in both the nymph and adult stages.

Some diseases are difficult to control chemically—thus the influence of sowing date and the selection of resistant varieties should be considered from the outset. The use of a large varietal collection as a starting point is often worthwhile.

The time from sowing to flowering is a function of moisture supply, fertilization, and plant protection, as well as of temperature and daylength. When the plant grows better, it will flower earlier. Time to flowering will vary over a period of 2 weeks or more, depending on soil fertility and soil moisture. The higher the soil-fertility level with optimum water, the earlier flowering will occur. In a crossing block, plant growth must occur as expected. Gross lack of uniformity of the field or severe insect attack can change the expected flowering performance of the crop, resulting in recovery of considerably less hybrid seed than anticipated.

Plants require the greatest amount of water at the time of flowering. The best seed set will be obtained if water is never limited during this period. However, selective application of water and fertilizer (especially if begun about 30 days after sowing) can hasten or retard flowering of all (or a portion) of a crossing block. The nick can still be improved to some degree at the flag-leaf (or early boot) stage if water is applied liberally to one plot and less so to another. (However, plants should never be starved for water.) Experience is required for effective use of water and fertilizer to adjust time of flowering; this is valuable knowledge.

Plant protection is important to ensure that the plants will grow as expected, as well as to prevent loss of developing seed due to head worms, bird depredation, or fungus development. Time of sowing should be adjusted to avoid seed maturation during the periods of expected high rainfall.

Field Layout

When organizing nurseries and yield trials, the same plot number should not be used on two plots during any season. If two plots have the same number, confusion is apt to arise following harvest, when a harvest bag can be identified only by plot number.

It is generally convenient to sow with ranges back to back as illustrated in Figure 4.9. Numbering follows a serpentine pattern that is convenient for making observations and recording notes in field books.

Yield trials should be organized so that entries of similar height and maturity are in the same trial. Tall

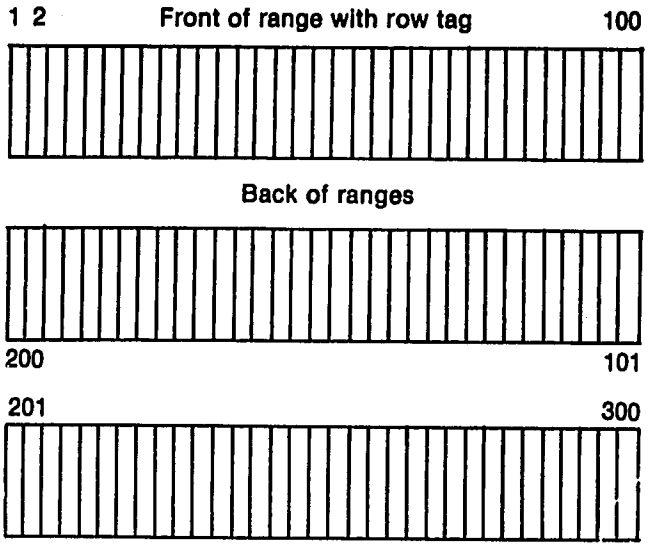


Figure 4.9: Serpentine pattern of numbering field plots.

plants shade and crowd out short ones so that the short ones fail to properly express their potential. A mixture of maturities in the same trial results in harvesting difficulties; harvesting a whole trial at one time may be impossible if maturities are widely divergent. Replications should be shaped as nearly square as possible to minimize soil variation. Each replication should be sown on uniform soils, even if they are not in immediate proximity.

Plots should fill a field; a small experiment should not be placed in the middle of a big field, thus leaving the rest of the field uncultivated. Wide borders between the edge of the crop and the edge of the field should be sown with an increase or bulk of the crop. Such measures will help keep the field uniform.

Time of Sowing: The effective use of some lines may depend on their photoperiod response. A photoperiod-sensitive type sown in October will flower, whereas the same variety sown in March may be much later or may remain vegetative. Generally, photoperiod-sensitive types sown from June to early February (at 18° N) will flower, whereas varieties sown in late February, March, and April may remain vegetative. Flowering occurs in the fewest days in the sowing period from October to early December. At 11° N, sensitive varieties sown in early April remain vegetative, where as at 18° N sowings made from mid-February to early March remain vegetative. Temperature may have an influence. Plants sown in November and December at Hyderabad, India (18° N and 535-m elevation) grow very slowly during the cool (December-early January) period. If the plants are in the seedling stage during this period, it may be very difficult to protect them from shoot fly.

The sowing date may be influenced by some insect or disease problem. The shoot fly population over much of the Deccan Plateau (southern India) increases in late July and August; sowing should be done in June or early July to avoid this pest. Some studies show that sugary disease is more severe in varieties flowering after September 25 than in those flowering before this date (in the central Deccan); thus, sowing so that flowering would occur before this date might be useful in avoiding the disease.

Long-duration varieties may be used so that sowing can occur before the shoot fly problem becomes serious, and so that grain formation and maturation occur after the rainy period. Sorghum grain on many varieties deteriorates in wet and humid weather; early stages of deterioration can be identified by tan, red, or purple (depending on plant color) specks on the seed—frequently at the tip of the grain. Sometimes small sooty black spots are found on the seed surface (*Phoma* sp). At times, the whole grain will become completely sooty black (*Curvularia* sp) or covered with a pink mold (*Fusarium* sp). The value of the seed is lost at this stage. Date of sowing should be adjusted to avoid coincidence of grain formation and maturation with periods of expected wet weather. Sowings made during the summer season on the Deccan Plateau of southern India are made as soon as temperatures become warm enough in mid-January to February. These plants flower during the hottest time of the year, and irrigation is frequently required to obtain full seed set.

There is an additional problem of head-worm damage if grain forms during wet periods. This is especially true of heads under pollinating bags—head-worm populations develop at an alarming rate, and much damage can occur before the problem is noticed. During wet and/or humid periods, it is best to remove head bags following flowering. The bags can be stapled around the peduncle to identify the pollination and to retain any information written on the bag. Head bugs (particularly *Calocoris angustatus*) that suck juice from the developing seeds can also be severe during humid wet periods.

Record Books

Field Books: Breeders use various record books; one much-used form has a temporary type of binding, i.e., pages are held between covers by means of screws. The pages can be cards of about 10 × 15 cm and can be filed at the end of a season. Standard 20 ×

28-cm sheets can also be used in such a binding. However, books that are held together by screws or pins do not lie flat when opened, and the row lines seldom line up across the center of the book. If such books are used, note taking will be easier if plot numbers are placed on both pages. The screws holding these books together prevent several books from stacking properly, and the books do not readily fit next to each other on shelves. It also is difficult to label such books for shelf identification.

Small bound books (10 × 15 cm) that fit into a pocket of a pollinating apron are very convenient. The small book has many advantages. It is easily carried in the field, there is less tendency for pages to blow in the wind than if pages are larger, and there is less glare from sunlight reflecting from the page. If the book is bound correctly, it will open with pages flat, so that the ruled lines join in the middle of the book; thus it is easier to follow one row from one edge of the book to the other. Lines denoting rows and columns should be printed in the book. Stocks of such books can be stored in bound form: plot number, pedigrees etc., must then be written into the books by hand (Plate 13-1). However, when required, pedigrees and plot numbers can be typed or mimeographed onto pages and later bound into books.

A high-quality paper should be used; a field book gets a lot of use and may get wet. A light green or blue paper would be easier on the eyes on a sunny day. If smaller books are used, pages will fit into standad carriage typewriters; they will also be of a size suitable for mimeographing. The paper should be light enough that several carbon copies can be taken on a typewriter—a good bond paper is usually tough enough to withstand weather and wear and is sufficiently thin for copies.

The sheet shown on Plate 13-1 has several advantages. The distance between row lines is equal to the double space on a standard typewriter. The printed page size (19 × 11 cm folded or 22 cm opened) is smaller than the standard 20 × 28-cm sheet and is trimmed after binding. No column heads are printed so that the same books can be used for any kind of experiment. Six to eight pages can be stacked and folded to make one section of the bound book. If the books are typed or mimeographed before binding, care must be taken to get the correct information on the right page. It is best to set up a model book, assigning page and plot numbers to each page (first and last plot number on each page) as guides for typing pages or stencils.

Plates 13-3 and 13-4 show pages that were designed and printed for breeding program use. Appropriate column space has been allowed and the column heads were printed. Pedigrees can be typed onto sheets that are bound later. Several difficulties have been noted in using these sheets for field books. They are big (hence difficult to use in the field) and impossible to fit into a standard carriage typewriter if unfolded (as would be necessary if carbon copies are being taken). The columns frequently have not been used for the purpose indicated, hence it would have been better if they had remained blank. (Generally there is more space than required so that much of the page area remains blank.) For these reasons, the smaller size shown in the first photograph (Plate 13-1) was adopted. Note that two formats are presented; one for yield trials and one for the nursery.

The pages shown in Plate 13-2 were developed by the wheat program of CIMMYT in Mexico, and are suited to the use of IBM equipment. These sheets are of moderate size, and are not folded when bound, hence are easy to read across the page (no discontinuity of the row at the fold of a book). The continuity of rows and columns is enhanced by alternating colors. Some column heads are printed and some are not. The paper would readily fit into a typewriter. Books incorporating these sheets could be pinned or bound between covers.

It is convenient to arrange columns on a page so that the plot number is close to the data to be taken; i.e., rather than having the sequence plot number, pedigree, origin, data, it is suggested that the order be origin, pedigree, plot number,data. It is easier to identify rows for note-taking with this arrangement.

In handling field books, common oversights include failure to include particulars about location, year, season, sowing dates, fertilizer, insecticide, irrigation schedules, rainfall, etc. Frequently, column heads are labeled only on the first page of the field book. If this page is lost, identity of some columns on subsequent pages may not be known and the information becomes useless. At times, days to flowering is recorded as a calendar date (20/9, for example), rather than as number of days from sowing or emergence (such as 65 days, etc.). If the date of sowing or emergence is not recorded and is forgotten, it becomes impossible to determine time to flowering. Rubber stamps can be used to label column headings; care should be taken to do a neat job. Numbering machines can be used to enter plot numbers.

Accession Book: An accession register (Plate 13-4) should be maintained. New seeds come in packets with identifying numbers (and possibly pedigrees) but usually little else. The receiving

PLATE 13. FIELD BOOKS

13-1. A small field book (approximately 16 × 11 cm), easily carried in the pollinating apron. Lines are printed on good quality (bond) standard sized (27.5 × 20.0 cm) paper. The distance between lines is equal to the double space on a typewriter; books can be typed and then bound. A small book is easier to use when it is windy, and there is less glare of sunlight from the page than if the book is big.

13-2. Field sheets designed for use with data processing equipment. Column heads are printed on the sheets, and adjacent rows and columns are highlighted by alternating bands of color—a great convenience while taking notes. The paper is not slick and soft colors (light yellow and green) are used to reduce glare from the sun. Such sheets are pinned between hard covers. Book size is approximately 26 × 20 cm.

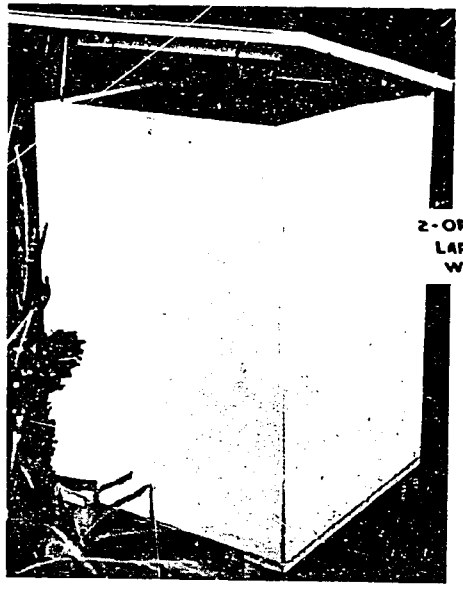
13-3. Large field sheet (28 × 20 cm after folding) used where the books are typed and then bound. Such books were found to be too large: they were inconvenient in the field, and a long carriage typewriter was required when pedigrees and plot numbers were typed on.

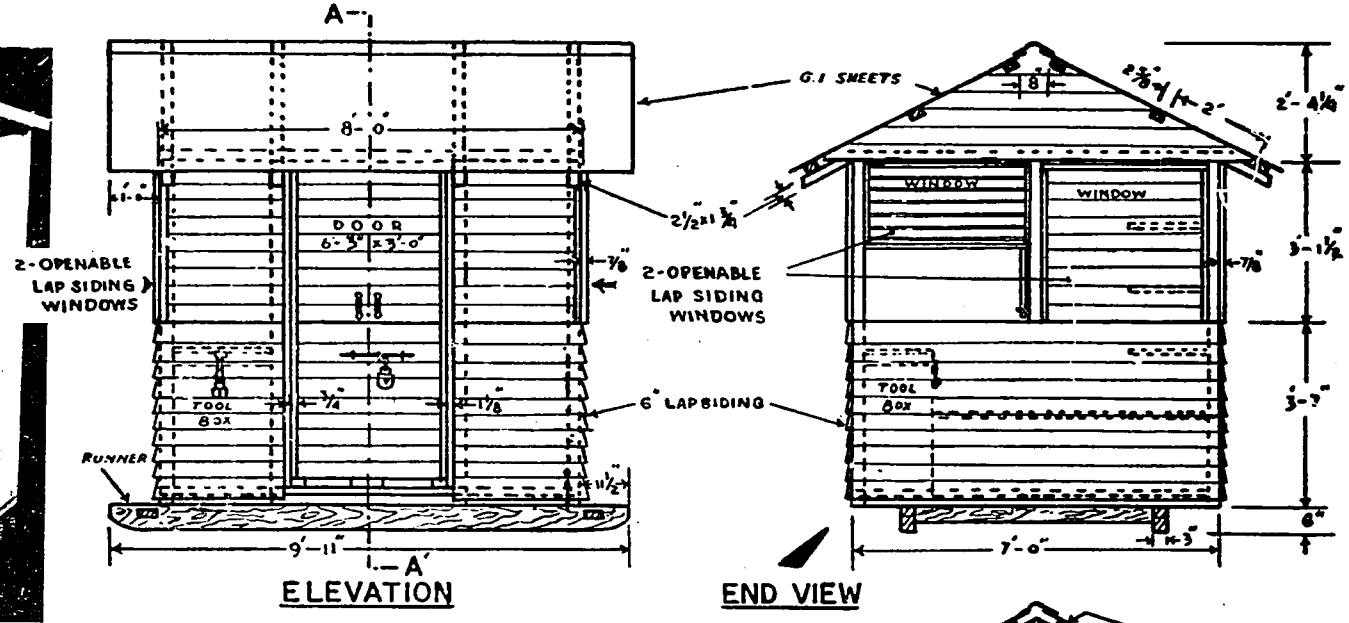
13-4 Printed page for the accession register; this page size (28 × 20 cm after folding) has proven satisfactory. Books are made large enough to include about 5000 entries and all notation is written in by hand. (When a book is completed it can be typed for future convenience and duplication). Column heads include: Date Received, Introduction Number, Pedigree, Originating Station, State, Country, Name of Sender, Year and Row Number (of nursery from which seeds came), and Remarks.

2

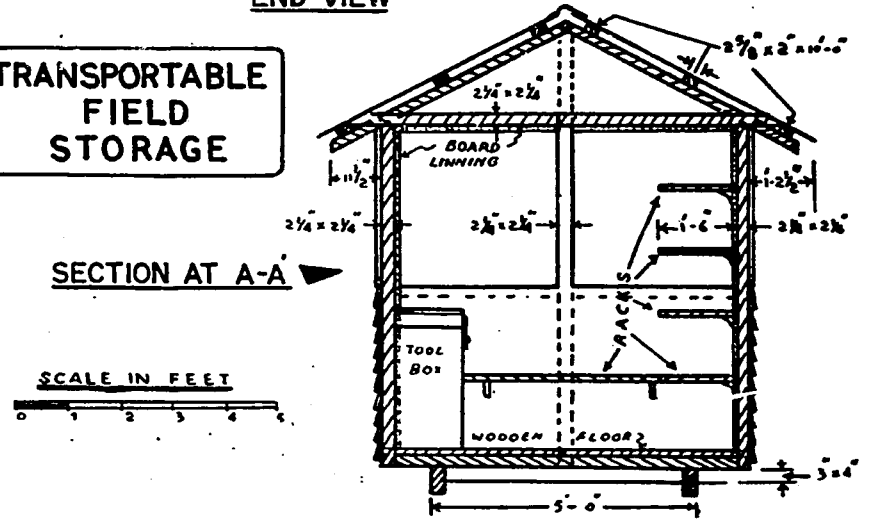
PLATE 14. THE FIELD HOUSE

This is useful for storing items needed for weeding, pollination, note taking, harvest, etc. Note the smaller field storage—a box with a lift-top lid for storage of pollinating bags and other small items.





TRANSPORTABLE FIELD STORAGE



breeder usually assigns a number to seeds of newly received varieties. An accession book should be bound and be large enough to list between 5000 and 10 000 items. Column heads in an accession register should include the address of the sender and comments. The accession register becomes the complete statement of all entries received, including the identification of the sender. Breeders make periodic reference to this register. The pedigree system of the receiving breeder may differ from that of the sender; thus it may be desirable to refer to the original pedigree, to acknowledge receipt of seed, to refer to comments about the variety, etc.

Dispatch Record: Column heads of this book should include date of dispatch, pedigree, and the name and address of the receiver. A breeder can use a dispatch book to readily indicate the varieties that he is sending most often and to whom. Keeping tabs on which seed has been sent to receivers can expedite seed shipment. For example, if seed is shipped to one breeder in a country and another wants seeds of the same pedigree, it may be best to redirect the seed request to the first breeder (this may avoid the delays and costs involved in phytosanitary and international shipment). Seed requests are not always specific—an individual may request seed of some lines because of some characteristic. The dispatch record can be used to avoid reshipping the same seeds, or the receiver can be advised if some previously shipped seed might be satisfactory for a particular purpose. The dispatch record is also an indicator of accomplishment and can be valuable in justifying program support.

Seed Inventory Book: Some seed in storage must be replaced occasionally for two primary reasons—the seed supplies may be depleted by requests, or there may be loss of viability in storage. Weighing seed when it is dispatched would help control the first problem; germination tests would monitor viability. It is probably not necessary to monitor all seeds in storage. An inventory of agronomically good lines, of lines superior as a source of resistance, and of lines to be held for long periods of time would probably be satisfactory. It would not be necessary to inventory items such as hybrid seed, seed from head selection, seed from segregating generations, etc. The decision to keep an inventory record could be made based on need. Some form of inventory is probably needed in established programs.

Row Tags

Each row should have a tag that is easily located. A tag fastened to a stake about knee high is most convenient. Inadequate tagging will cause loss of time and increased error. (See Plate 12, 4-10.)

Row tags should be colored for easier location. Yellow is a good color for tags; it contrasts well with the green foliage. The tags should be of strong paper to withstand weathering. If a wire or string is used to fasten the tag to a stake or plant, an eyelet should be fixed into the tag to keep it from tearing during rain storms.

If the only information on a tag is the row number, the tag can be stapled to a stake and placed in front of the row. This is a very convenient way to label, as no time is lost looking for a row tag. However, pollinating instructions can be marked on a tag, and then (as pollination proceeds) an indication can be made each day as to what has been done in a row. For example, the instruction may be O (10) (self-pollinate 10 plants). On the first day three pollinations may be made, so the worker making the pollinations would mark 111 on the tag; on the second day, five more pollinations might be done, so the pollinator would add five marks (eight total); on the third day, the pollinations might be finished, so a line could be drawn through the instruction. Other instructions can be included as indicated in Plate 12 (p. 110). As illustrated, row 27 is to be pollinated by rows (53), 9(10), and 3(4), requiring 3, 10, and 4 crosses respectively. Pollen from row 27 is to go onto rows 15 and 17, requiring four and three pollinations, respectively. After the pollinating instructions have been completed, the tag can be folded and a paper clip placed to keep the fold closed. Plot numbers can be written on tags or stamped on with a numbering machine. The number should be placed on top and bottom of both sides of the tag. If one side of the tag is damaged, the number is still readable on the other side; also there is no need to turn the tag around to see the numbered side. At harvest time, the tag can be torn in half—the lower half going into the harvest bag, thus insuring that identity of the bag is maintained even if the tag on the outside of the bag is torn away.

Field House

During a cropping season, many hand tools, paper bags, pollinating aprons, emasculation equipment, etc., are required in the field. A field house of the type pictured in Plate 14 is quite convenient for storage (and is a good shelter from short rains). It should be fitted with shelves convenient for storage of items such as pollinating bags; drawers to hold small items such as staples, paper clips, marking pencils, etc; and large windows that open to keep

the house cooler and facilitate handling of stored items. The house can be locked up at night. It should be built on skids so that at the end of a season it can be pulled to a storage area or to another field.

A small field house such as this saves a lot of time and effort otherwise spent carrying equipment back and forth each day and helps maintain a supply of often-used items. If the program is large or scattered, more than one such field house may be useful (approximately one field house for each 3 or 4 ha of experimentation).

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SECTION 5
THE SEED INDUSTRY
ROLE, ORGANIZATION, AND DEVELOPMENT

Sorghum is commonly grown under harsh conditions, and under such conditions hybrids are frequently higher yielding and more stable than ordinary cultivated varieties. However, the problem of seed production remains a major constraint to the use of hybrids.

Traditionally, departments of agriculture produce seed and distribute them to farmers; such seed may be produced at research stations (as an added task of the breeder) or on special farms organized by the department for seed production purposes. The operation is relatively simple and straightforward, requiring a relatively minor input from the department.

Beyond providing this annual seed supply, the traditional seed production units are not concerned with what actually happens to seeds that farmers sow. Many farmers keep their own seed—periodically buying from an outside service—and many farmers buy from neighbors or from a local market. There is no quality control, and seed as a commodity may be very poor.

The sorghum breeder should be interested in seeing that his hybrids are used by the farmer. On the surface, it might seem a simple process to produce and distribute hybrid seeds in much the same manner as has always been done for varieties. However, the situation is considerably more complicated—requiring careful study and consultation. The production and marketing of hybrid seeds provides a vehicle on which to build an industry with quality control and extension components. If done properly, the continuous availability of quality seeds can be an important force in shifting away from a traditional agriculture.

This section does not attempt to describe all the details of establishing a seed industry. It is meant primarily to indicate the nature and complexity of establishing a seed industry—to increase the sorghum improvement worker's awareness of what may be involved. Appendix I provides additional information about development of the seed industry.

During the 1960s, field staff of the Indian Agricultural Program of the Rockefeller Foundation contributed to the development of a seed industry in India. A number of the papers from this project have been generalized for inclusion in this section; acknowledgment is due to Johnson E. Douglas, Wayne H. Freeman, and Guy B. Baird. The original papers were prepared in limited numbers for a special purpose and are no longer available.

The Role of a Well-Organized Seed Industry

Adapted from a Paper by Dr. Guy B. Baird

Plant breeders and specialists in related agricultural sciences have developed high-yielding, adapted varieties or hybrids of the major cereal crops. These improved strains have made a major contribution to increased food grain production in India. Their continuing contribution will depend on adequate supplies of high-quality seed being available to the cultivator. A well-organized seed industry is needed to ensure that these conditions are met.

The seed industry is a key facet of modern agriculture. To obtain and sustain high crop yields, the efficient farmer must use seed with a high yield potential and he must modify the plant environment to favor the development of the crop. The modern farmer modifies the plant environment by utilizing equipment and materials from various agro-industries; examples are tractors, improved tillage implements, fertilizers, pesticides, and insecticides. The farmer also modifies the environment by management practices, such as drainage and irrigation, to provide optimum soil moisture conditions for the high-yielding crops.

What is a Seed Industry?

A seed industry supplies the seed needs of the farmers and is composed of independent growers, producers, processors, and distributors. To achieve economy and efficiency a single enterprise may combine all of these functions into one operation. As an illustration, the hybrid maize seed industry in the United States produced over 350000 tons of seed for annual plantings on more than 32 million hectares of land. This was not a planned industry, although it was based on the results of research from the federal and state experiment stations. The "industry" was composed of well over 500 producers, who grew seed on farms ranging in size from 5 acres to 1000 or more acres. It grew from an infant industry in 1930 to an industry supplying seed for 50% of the maize acreage 10 years later. Today it supplies seed for 100% of the planted acreage. The producers sell directly to the farmer, not through government channels. The seed is produced, dried, shelled, cleaned, sized, treated, and stored at the producer's expense. Profits made in the first 10 years of the industry enabled a substantial number of seed companies to develop full-scale research programs of their own, with research efforts oriented to filling consumer needs.

Companies in this loosely defined industry increased the sorghum acreage in the USA from no acreage planted to hybrid seed in 1954 to 100% planted to hybrid seed in 1960.

It is apparent that a relatively free private system of seed production has been able to meet the demands for good quality seed. If a seed production system is soundly based, it should be able to provide adequate seed during a transition period from government production and distribution to private production and distribution.

Seed in Traditional Agriculture

In traditional agriculture the farmer can be largely independent in terms of his inputs. He, his family, and his farm animals provide (directly or indirectly) most of what he needs in his farming operations. This applies to seed, fertilizers, farm implements, and weed control. But diseases and insect pests may exact heavy tolls, because the traditional farmer is unable to cope with them.

In traditional agriculture, seed commonly is part of the overall production of the crop of the farm. Normally, a planting would not be made specifically for seed production. In some cases, the farmer may do limited selection to obtain a desired type or improved quality from his overall production. Over a period of time, good farmers who conscientiously select material for seed from their production may materially improve their seed in terms of quality and yield potential. However, in general, a very limited scope exists for crop improvement under these conditions.

The traditional farmer is limited in his capacity to make progress in crop improvement, both in terms of the genetic make-up of his crop and in his ability to modify the plant environment. Typically, his crop has a relatively low yield potential. It has been grown for many generations under conditions not conducive to high grain yields. Through natural and deliberate selection, strains capable of thriving under the conditions of traditional agriculture have persisted. The genetic variability has become quite

narrow, and the scope for substantial improvement is correspondingly restricted. With this type of genetic material (varieties of crops) there is only a limited incentive to make the plant environment more conducive to high crop yields. Use of chemical fertilizers, irrigation, and other improved farm practices also may be unattractive because of inadequate economic returns.

Seed in Modern Agriculture

The plant breeder, with the help of his fellow agricultural scientists, can develop new varieties or strains with a capacity or potential for high yields. He can also incorporate new materials into these—factors that affect grain quality and insect pest and disease resistance. Thus, agricultural scientists provide the farmer with improved crops that can help him move from a traditional to a modern type of agriculture. With these improved crops, the progressive farmer will find it profitable to use other inputs of modern agriculture, including fertilizers, better farm implements, and better soil, crop, and water management.

But what about the seed for these improved crops—will the farmer be able to produce his own seed in the traditional way? Theoretically, he could produce this seed; however, he may find it impractical—for several reasons. In the case of hybrids, production needs such as plant isolation, experience, and attention become prohibitively expensive and inefficient for the farmer growing seed for his own use. With self-pollinated improved crops, the farmer may find it satisfactory to take his seed from his regular crop. However, in such cases, he is likely to find that mixtures occur after several seasons, and he will want to replenish his seed with stock of high genetic purity. Further, when better improved varieties are developed, he will wish to discard his previously used variety and obtain the newer.

It is clear that the farmer in modern agriculture must have access to seeds of the high-yielding hybrids and varieties. A basic concern is that of how to provide these seeds to the farmer.

Seed Production

Seed production today is a specialized and essential industry. It is analogous to fertilizer or pesticide production, to the manufacture of farm implements and crop processing equipment, and to the development and production of weedicides. In each of these industries, specialists provide the farmer with the inputs necessary for sustained high-level crop production. This is in marked contrast to traditional agriculture, where the farmer took care of most of his needs on his farm.

The seed industry is made up of several components, including research, production, quality control, and marketing. As in other industries, both the private and public sectors are involved.

Research

Improved seeds are a result of research. Agricultural scientists collect the germplasm of the crops to get as much variation as possible. These collections are evaluated, and combinations or crosses are made to obtain new strains with the desired characteristics. Promising strains are tested in the areas where they might be used if proven suitable. When a new strain is developed and performs well enough for use by the cultivators, it is proposed for release by the plant breeder who developed it. The small amount of seed of the new strain (or of the lines going into the new hybrid) is referred to as breeders' seed.

Concurrent with the development of the new strains, supporting research shows how to manage the strain to capitalize on its yield potential. Such research commonly includes insect pest and disease control, plus fertilizer and water requirements.

Production

After the development of a new strain, the small amount of breeders' seed must be multiplied so that the farmer can purchase it. Seed production organizations are required. The initial stage of the production of breeders' seed is referred to as foundation seed production. Foundation seed production requires a relatively high degree of competence to meet quality requirements. This seed is used to produce the commercial seed to be used by the farmer for his crop.

Production of commercial seed is a specialized operation that calls for a higher level of competence than can be provided by the average farmer. Producers of commercial seed are specialists in that business and are expected to produce a reliable, high-quality product.

Quality Control

When a farmer wishes to buy improved seed, he may find that it is available from several sources. It is important that information be readily available to

him for judging the quality of the seed. Seed laws and seed control agencies are established to insure that seed on the market will meet certain quality requirements. These laws and agencies make it difficult or hazardous for a seed producer to market inferior seed. They protect the farmer and help develop a seed industry with high-quality seed as the primary product.

Seed certification is commonly an important adjunct of the seed industry. The process, which normally is voluntary, places emphasis on the genetic purity of the seed, and on other quality considerations. Certified seed, or its equivalent, is a premium seed; a seed that merits and commands a higher price on the seed market.

Marketing

The transfer of the seed from the producer to the farmer (i.e., the marketing of the seed) is a vital link in the seed industry. Marketing may be a relatively simple process in which the farmer purchases directly from the seed producer. It is often more complex, however. A single seed producer may have produced the seed under contract to a parent seed company or corporation. The latter may produce seed in several parts of a state or in several states. The market for the company may cover an entire state or all of the country. The farmer may buy seed from this company through one of its marketing outlets, which in turn may have seed as only one of its several products. In all cases, however, efficient marketing means ready availability of the seed to the farmer.

Although the facts seem obvious, farmers must be impressed with the importance of the improved seed as a key input in modern agriculture. The farmer must be convinced that this improved seed, when used properly, can be a profitable investment. Thus, the importance of agricultural extension or farmer education.

Industry Organization

The seed industry has several distinct, but highly related, components: research, production, quality control, and marketing. In a well-organized seed industry, each component must be given appropriate attention, and the components must be linked and integrated.

Both the public sector and the private sector have important roles to play in the seed industry. Obviously, the public sector institutions are directly involved in the development and maintenance of quality standards, in interstate marketing, and in farmer education. Research is also an important function of national and state or regional agricultural institutions. However, both public and private sector institutions concerned with seed may be involved in research, in farmer education, in foundation seed production, in production of certified and commercial seed, and in marketing. The important consideration seems to be the development of conditions and an atmosphere that will stimulate the production and use of high-yielding, high-quality seed. The realization of this goal involves a close-working relationship and understanding between public and private sector institutions.

Within a very short period, India made remarkable progress in the development of a well-organized seed industry. Through research, high-yielding strains of all of the major cereal crops were made available to farmers. The National Seeds Corporation has capitalized on these areas of research by arranging for the production of the necessary foundation seed. It has also played a much broader role in the development of the Indian seed industry. It has encouraged producers of commercial and certified seed, has trained seed production and certification personnel, and has acted as a certifying agency until state certifying agencies were established. A Seed Law has been enacted, and an India Crop Improvement and Certified Seed Producers Association has been formed.

A Quality Seed Production and Distribution Program

Adapted from a Paper by Johnson E. Douglas

Production of high-quality seed is the primary objective of a seed program. A seed act that provides for a seed law enforcement program and a comprehensive seed certification program for improved varieties and hybrids will encourage greatly increased quantities of good seed for the farmer.

Each country must insure that there are sufficient production and distribution facilities throughout the growing region of a crop. Plans must be developed so that the best use can be made of both governmental and nongovernmental agencies. Their functions should be complementary so that the maximum quantity of good-quality seed reaches the cultivator. At the 1962 FAO meeting of the Technical Committee on Seed Production, Seed Control and Distribution, the following summary statement was made:

> It was felt that, in developing countries, seed production and seed distribution should gradually be taken over by non-governmental agencies, such as seed cooperatives, seed growers associations, and private firms; provided an adequate level of quality control could be maintained.

A committee was appointed in India in 1960 to develop the "blueprints" for an organization that would assure the rapid multiplication and distribution to cultivators of dependable, high-quality supplies of seed of improved maize hybrids (and subsequently of other crops). These blueprints set up a five-step guide to insure proper organization of a seed program.

1. Organization for the production of foundation (nuclear) seed must be developed. Because of the quality requirements and since provision of adequate supplies of foundation seed is in reality a service enterprise, these organizations should be closely guided by plant breeders and extension seed specialists, and probably should always be self-supporting agencies of the National Seeds Corporation.
2. A seed industry, operating in the private sector and stimulated by competition and the profit motive, must be developed to produce, process, and market the seed of double cross maize hybrids, as well as of improved hybrids and varieties of other crops.
3. Seed certification agencies must be established to operate independently of direct government control, of the foundation seed organizations, and of the private seed industry.
4. Seed laws must be passed and seed law enforcement agencies of the state governments must be set up.
5. An aggressive educational and demonstrational program on the use of maize hybrids and other improved seed must be carried out by the state, district, and block extension seed specialists who have seed improvement as their principal work.

To implement a program of this type, action is required in a number of areas. Much developmental work and emphasis is needed in the actual production and distribution phase of the program. Some basic requirements must be met to help this portion develop and grow with government encouragement, but without the government's actual participation:

- Superior varieties and hybrids of many crops should be available for multiplication.
- Hundreds of seed producers and dealers should learn new skills and develop new concepts of "good seed."
- Extra capital must be available for producing, processing, storing, and distributing seed.
- Good-quality seed must be produced and sold.
- Special equipment must be available to seed producers and dealers to help them produce a quality product.
- A strong educational program is needed for the seed producers and dealers as well as for concerned governmental agencies.
- Opportunities should be available for many individual seed firms to grow and develop.
- Sufficient incentives must be available in the program to justify a person or firm taking the risks necessary to develop a seed business.
- People must be found who are sincerely interested in selling good-quality seed and whose integrity is of the highest order.

Implementing the Basic Requirements

To utilize and improve all available resources and apply the basic requirements outlined above, the various stages in the seed multiplication process should be analyzed.

Breeders' Seed: The institutions and organizations involved in the breeding programs throughout a country have specific responsibilities in addition to the development of improved varieties and hybrids. These responsibilities include:

- recommending specific improved varieties and hybrids for release;
- providing general and morphological descriptions of the varieties and hybrids being released;
- maintaining adequate stocks of pure seed of the released varieties and hybrids so that the multiplication program will have a constant supply of reliable seed (breeders' seed);
- providing assistance to the seed certification inspection staff in their training so that they can competently identify improved varieties and hybrids that are in the seed multiplication program.

Foundation Seed: The production of foundation seed is a midstep between the breeder and the producer of commercial seed. The foundation seed stocks agency takes breeders' seed from the research organization on a periodic basis and increases this seed (usually under certification) and markets the foundation seed produced to commercial seed producers. It is not necessary that the

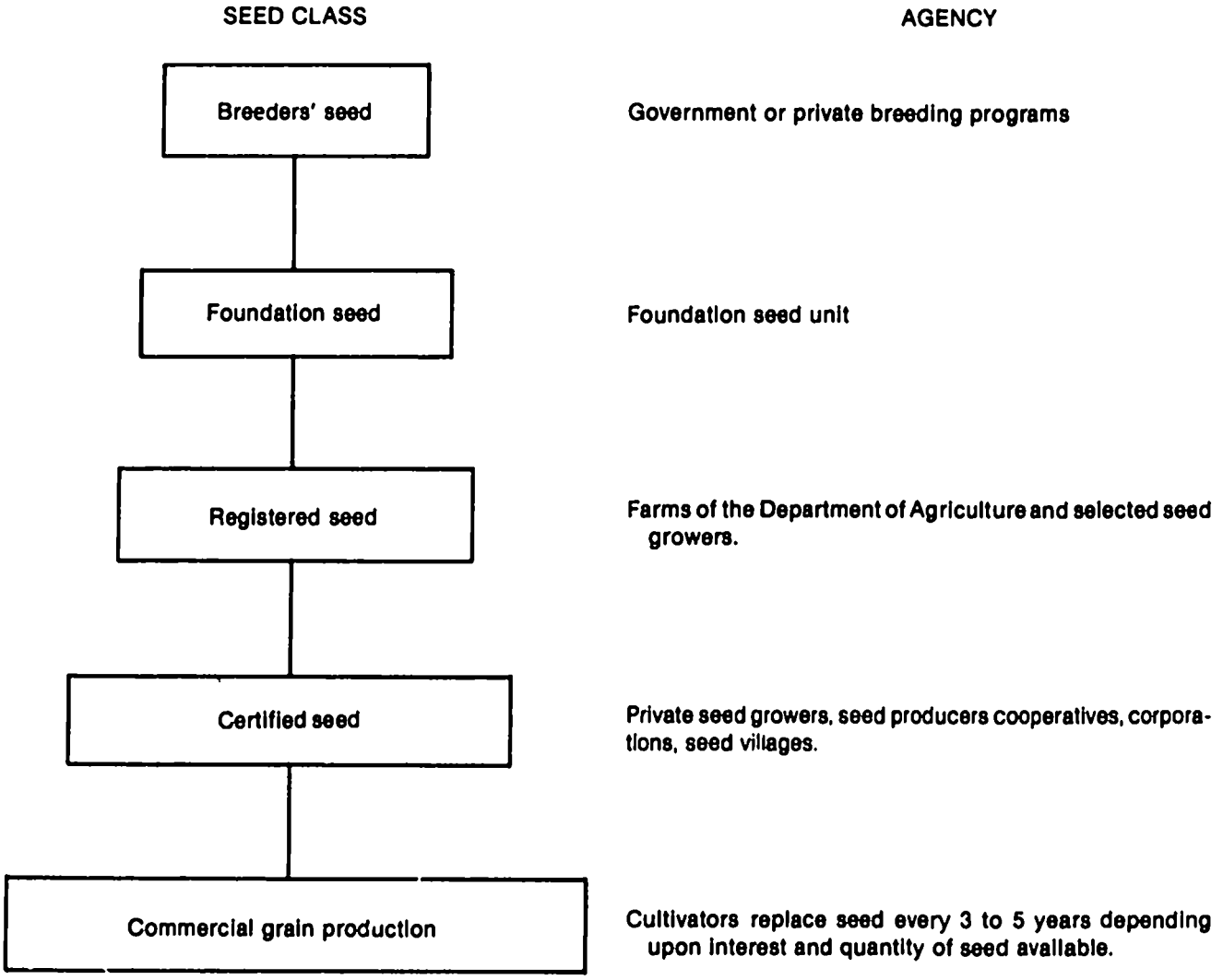

Fig 5.1: Production and distribution of certified seed of self-pollinated crops.

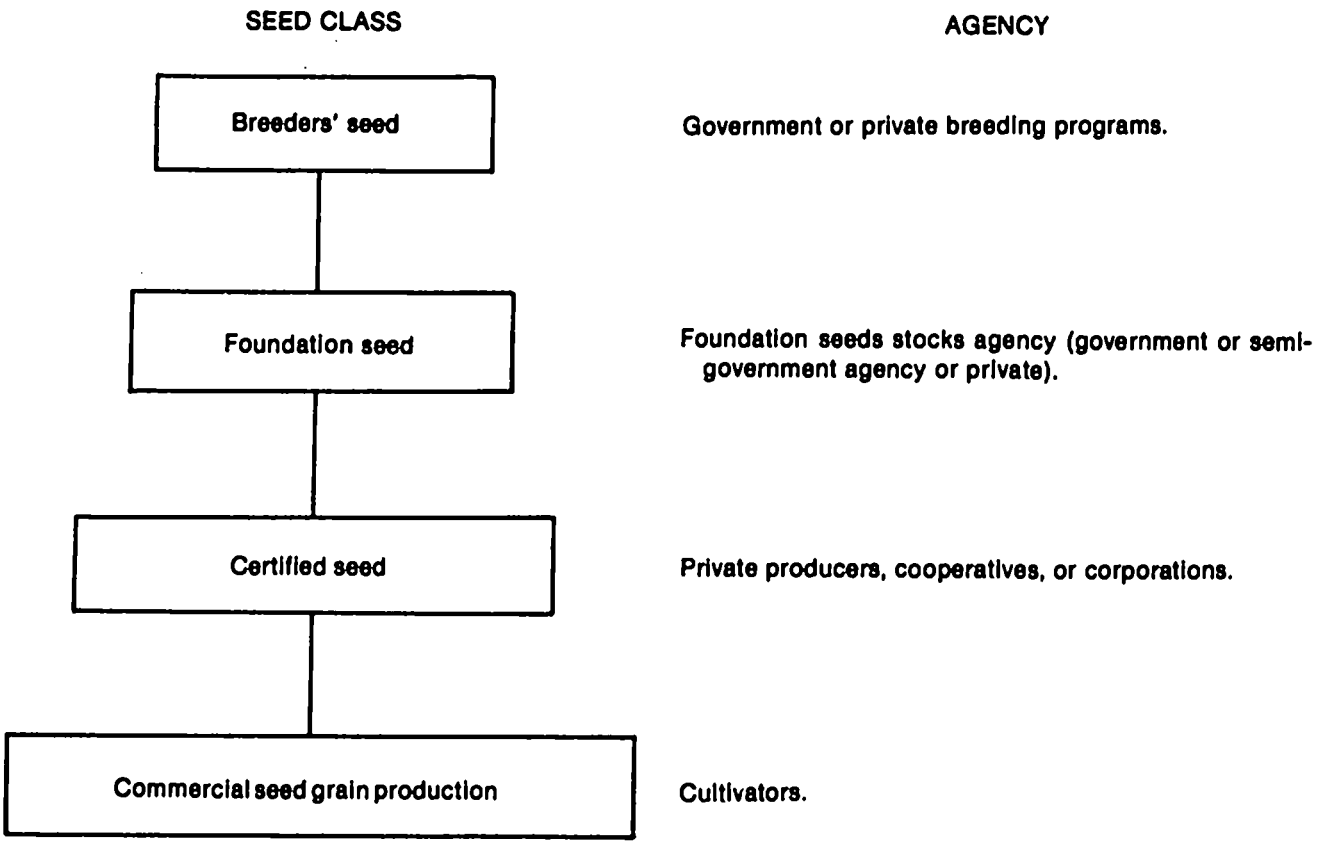

Fig 5.2: Certified hybrid seed production and distribution.

foundation seed stocks agency sow every field from breeders' seed, but it should go to breeders' sources periodically (as necessary to maintain purity and type in the foundation seed).

Registered Seed: The foundation seed of self-pollinated crops produced through the foundation seed stocks agency could be further multiplied as registered seed on state farms by seed growers operating on a contract arrangement with the Department of Agriculture, or by private seed producers planning to multiply the registered seed through the next stage of certified seed for distribution (Fig. 5.1).

In this example, the Department of Agriculture would be responsible for finding individuals, corporations, cooperatives, and others who would agree to buy the registered seed and multiply it so that a large quantity of certified seed would be produced and distributed to farmers. As the program grows, the department would develop an ever increasing number of such individuals and firms upon whom it could rely for completing this final stage of multiplication. The individuals and firms would be purchasing registered seed or foundation seed on a yearly basis for further mutiplication to supply adequate quantities of certified seed. Every encouragement should be given to these individuals and firms to be responsible for their own sales and distribution.

In the case of hybrid seed, foundation seed would be used for producing certified seed (Fig. 5.2). However, the foundation seed would be sold to individuals, corporations, cooperatives, and others who have decided to make hybrid seed production a business.

Since all of this seed would be provided to qualified individuals and firms who would be interested in and capable of making another seed increase, there would be no need to subsidize it. It would be sold to them at whatever price was necessary to produce the seed and still gain a reasonable profit for the registered or foundation seed increase program. The Department of Agriculture should not suffer any loss on a long-term basis. Of course, an initial investment for improving facilities would probably be required.

Certified Seed: Quality must be the primary emphasis in the production of breeders', foundation, registered, and certified seed. All stages of

seed multiplication must meet certain basic seed certification standards (Fig. 5.3). Good-quality seed of improved varieties and hybrids becomes doubly important in the final certified seed stage, because it is at this point that the farmer must be satisfied that the seed he buys will perform well and profitably.

This stage of the seed multiplication and distribution job should remain open to participation by many different individuals and groups. The opportunity for diversity and the resulting competition can help assure an efficient program that is quality oriented (Figs. 5.3 and 5.4).

Resources available within each district, province, state, etc., will determine the final shape of a certified seed multiplication and distribution program. A whole range of cooperatives, seed producers, seed dealers, local corporations, and seed villages should play a part. In some areas one or two of these groups may play a leading role, while in other areas the success of the program will depend on all segments.

Regardless of which group or combination of groups is involved in a particular area, three main processes are involved in accomplishing this task (Fig. 5.4). They are:

- seed growing;
- seed processing, storage, and wholesale seed distribution; and
- retail seed distribution.

The individuals and organizations involved in this program may perform any, or all, of these activities. The key to success is in keeping the various approaches flexible from one area to another, so that the program is not bound to any one particular

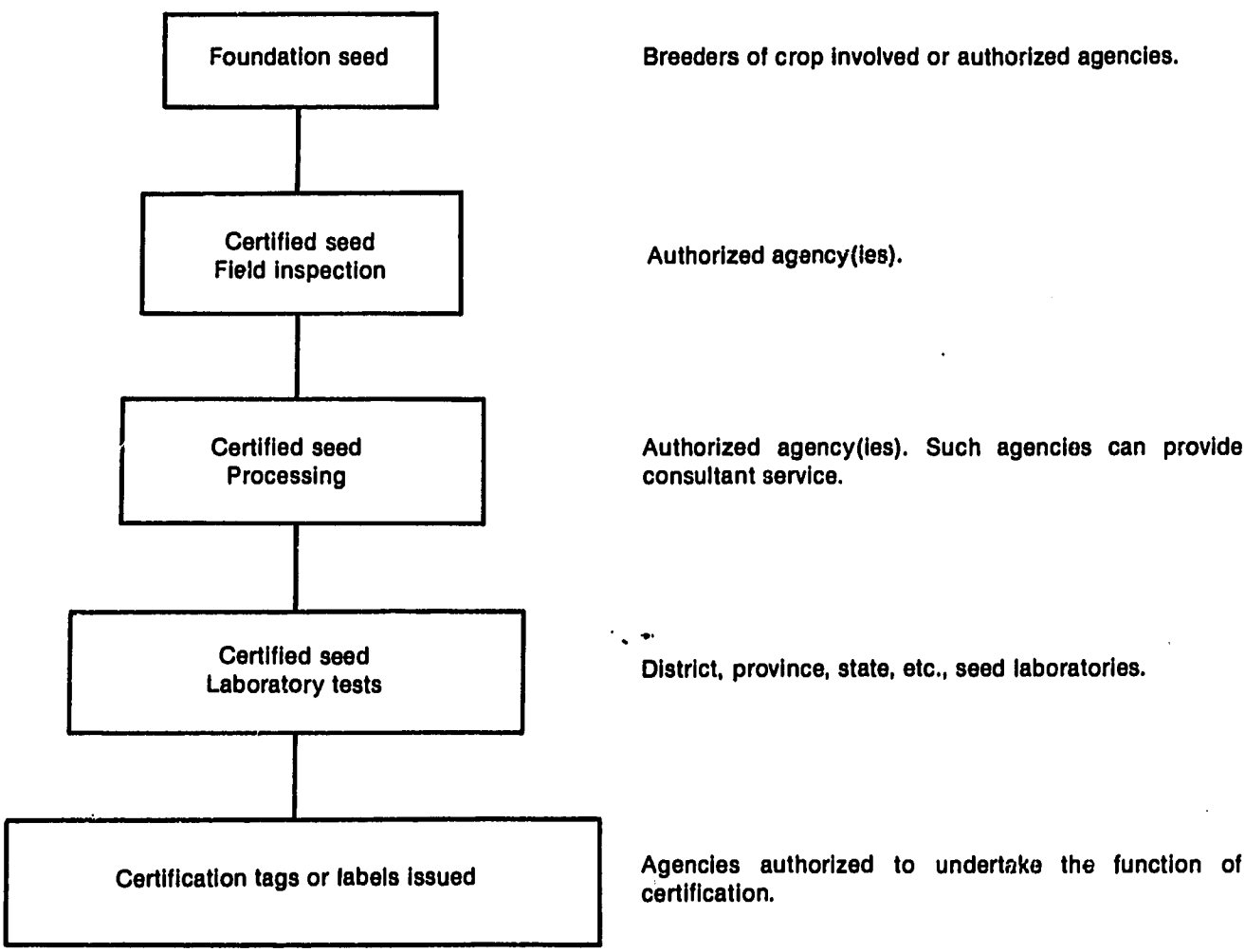

Fig 5.3: Certification of seed production.

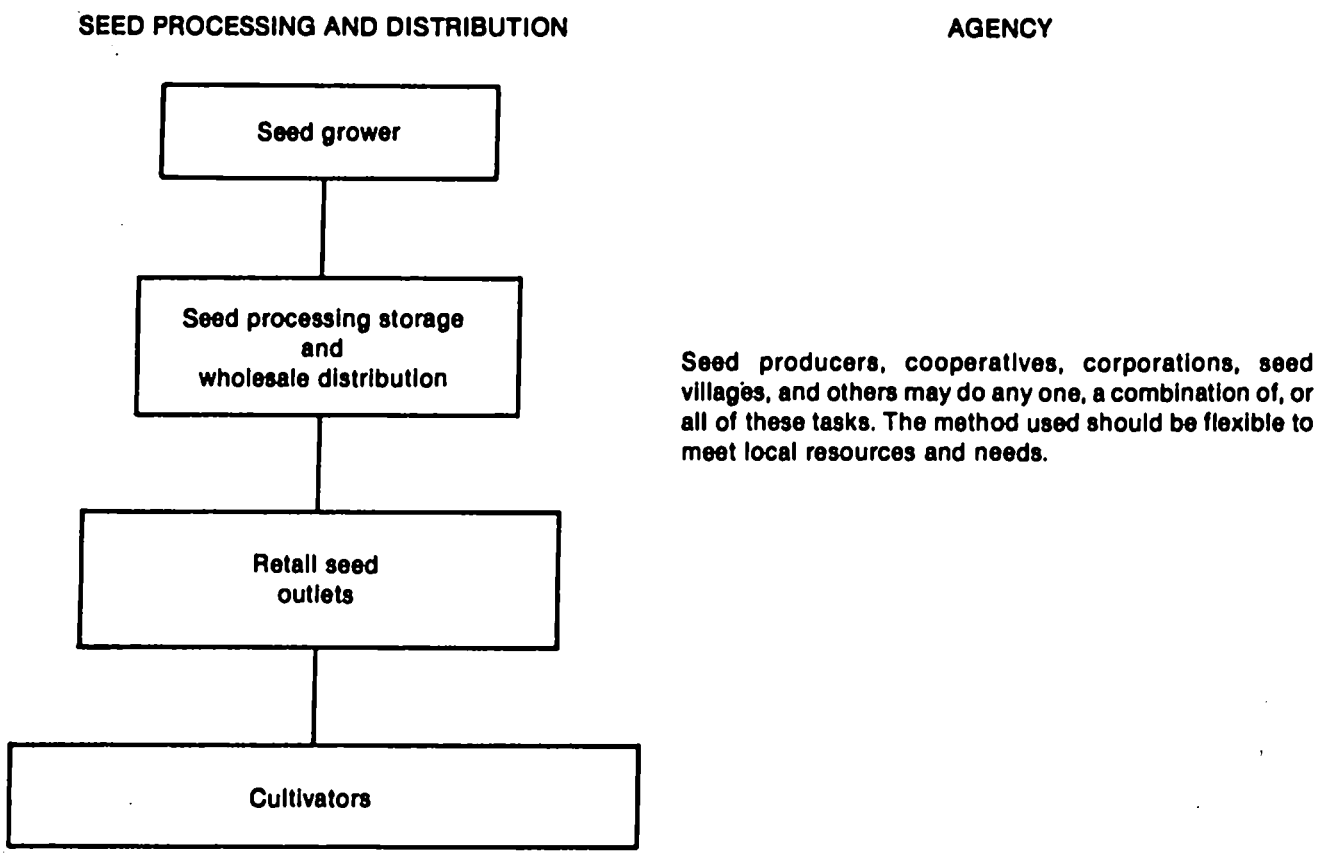

Fig 5.4: Process of seed multiplication and distribution.

technique. The approach used should depend upon the resources available locally. Regardless of the method of production used, the seed act (either the voluntary seed production program or the mandatory seed control portions of the act) will assure seed quality.

Any group of individuals involved in seed production and distribution should build a program based on sound business principles. Good seed is a basic agricultural input that should pay its way if the program is to be established on a sound basis and grow in the future.

Aspects of Seed Multiplication and Distribution

Seed Growing (Fig. 5.5): Many seed growers will be needed throughout a country. However, these persons should remain with the program for some time so that they may gain experience and be able to make their individual contributions, rather than be dependent upon the seed development staff and the Department of Agriculture. Before planting, a seed grower should make plans for his seed processing and for the sale and distribution of his seed. Generally, it will be advantageous if seed growers are located in areas near the processing centers.

Some seed growers may wish to do all of these jobs themselves; this would be especially true with many hybrid seed growers. The majority of them, however, will find it advantageous to operate through a contract made in advance for the distribution and disposal of their seed. This contract should be made with a cooperative, seed producer, or local corporation capable of processing, selling, and distributing the seed. The seed development staff of the Department of Agriculture or the field staff of the Foundation Seed Unit should be certain that this phase of the program is completed before the foundation or registered seed is sold to the seed growers for multiplication.

Seed Processing: Seed processing units are needed throughout the country. These units could be operated by one of the following:

- good cooperatives that are willing to act as wholesalers in the total seed program;
- private corporations operating in local areas;
- present or future vegetable seed dealers who are interested in expanding their programs.

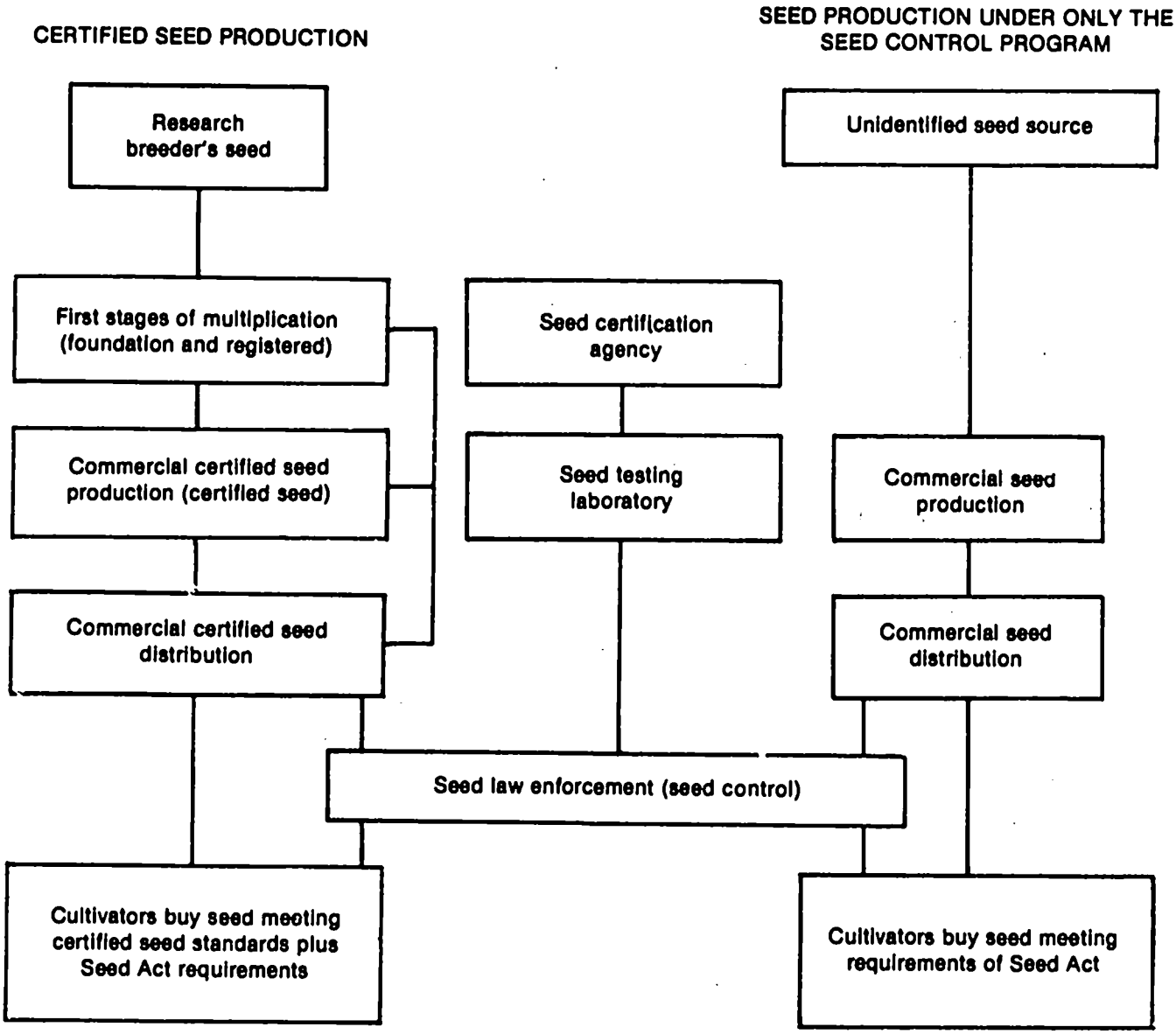

Fig 5.5: Seed production with and without certification.

These units could act as contractors with seed growers and as wholesale buyers and collection points for the certified seed produced. They will also probably develop their own wholesale and retail seed outlets. Such individual units could be encouraged by the availability of adequate credit to help develop their seed processing and storage facilities.

The seed development staff could assist in locating individuals and firms that might do this work, and could guide them technically. They also could encourage good working relationships between the seed growers and the seed processing centers.

Retail Seed Distribution: Efforts should be made to locate many outlets for the sale of the certified seed. The seed-processing units would probably sell a certain amount of seed directly, and would search for retail outlets for their seeds as well.

Many cooperatives, even though they may not be interested in actually processing the seed, should be willing to sell seed after it is completely processed, bagged, and tagged (provided there is a sufficient margin of profit to make the business attractive). Some local growers might also serve as village seed dealers. Even though not involved in

seed processing, seed shops (as well as other shops handling agricultural supplies) in various villages and towns could also be seed retail outlets.

It should not be necessary (or desirable) to provide a subsidy in this phase of the program, because good quality seed would be made available. This should be a sufficient inducement to justify a price high enough to support the extra effort and expense that are involved in its production, processing, and distribution. A review of these points, included in a 1962 FAO report, states,

> Improved seed programs are subsidized because it is believed that the cultivator will not or cannot pay the premium price needed to support a high-quality seed production and distribution program. However, seed subsidy in its various forms does not lend itself to the development of a sound seed industry, because (1) it becomes primarily a credit or loan program rather than a high-quality seed program, (2) the volume of seed produced and distributed is limited by government appropriation rather than by need or by supply and demand, (3) a private seed industry cannot emerge because profit or balance of returns equal to costs is not possible, (4) the agricultural officers in charge become supply clerks rather than educators or demonstrators of good seed, and (5) once established, a subsidy program for seed is difficult to eliminate.

The personnel involved in developing the seed processing, storage, and wholesale distribution units might also develop a sales organization to work through the district in their area. The sales organization could include a sales manager, district salesman, and the retail seed dealers as mentioned earlier.

The seed development and extension staffs, especially the seed development staff, would also have numerous responsibilities at this stage. They could include:

- supplying cultivators with lists and information on sources of improved varieties and hybrids;
- preparing demonstrations;
- organizing field days and special meetings centered around an emphasis on good seed of improved varieties and hybrids;
- organizing training meetings for operators of seed processing centers, for seed growers, and for those involved in the general distribution program. This work would differ from the field inspection and seed sampling responsibilities that would be done by the relatively small, well-trained staff working on the seed certification and seed control program.

Seed Production and Distribution Outside the Seed Certification Program

Large quantities of seed that have been produced without the close care and supervision needed for certified seed will continue to be planted. Much of this, in the case of self-pollinated crops, will be the cultivators' own seed. Some of it will come from seed merchants who do not have improved varieties for certified seed production.

Establishment and enforcement under the Seed Act of the rules and regulations for minimum germination and purity limits provides a means for improving the quality of all seed sold, not just the certified seed.

Most of the points covered under "Aspects of Seed Multiplication and Distribution" for certified seed would also be applicable to multiplication and distribution of seed outside the program. The individuals and businesses involved in this phase of the program should assume more responsibility in assuring that they are producing and selling a quality product at least equal to the requirements under the Seed Act.

The extension staff has a responsibility to:

- acquaint all who are dealing in seeds with their rights and obligations under the Seed Act, and
- encourage cultivators to test their own seed for germination, or to send a sample to the seed testing laboratory for testing.

References

FAO. 1962. Report of the FAO Technical Meeting on Seed Production, Control and Distribution. Rome: FAO.

Section 5 continues next page.

Developing A Seed Industry

Adapted from a Paper by Wayne H. Freeman

In a developing economy, agencies often do not understand their roles and relationships. Even though programs and projects are written, the problems of implementation and interpretation can be great.

The concepts of competition and the profit motive have been cited as characteristics that would provide a necessary stimulus to the development of a seed industry. Experience in the development of a hybrid seed industry in Europe (Jenkins, FAO Report, 1953) has indicated that a lack of competition, created by cartels and government interference, retarded the development of a seed industry there. Some of the more traditional concepts—suggestions that seed be produced by the Department of Agriculture and distributed as a community contribution through an extension agency—do not apply to the production and marketing of hybrid seed. A quality seed production program requires step-by-step implementation. These functions are listed in Table 5.1.

Table 5.1: The various functions of the seed industry and its associated agencies.

Function	Agency or agencies
1. Research (central, regional, state co-ordinated)	Government (or private).
2. Variety release	State and/or Central Variety Release Committee (for products of public breeding research operations).
3. Foundation seed production	Foundation Seed Stocks Agency and/or private producers who have their own hybrids.
4. Seed production and distribution	Private producers who market seed to cultivators
5. Seed certification	Recognized agency(ies) to undertake certification
6. Seed regulatory work	District, province, and central departments of agriculture
7. Extension	Agricultural universities, and/or state departments, and/or community development blocks, and/or private seed companies.
8. Credit	Cooperatives, banks, etc.

The difference between the more traditional approach and the one outlined in Table 5.1 is that in this approach public agencies take primary responsibility for quality control and extension aspects, while private agencies are primarily involved in production and marketing aspects.

Several examples illustrate the kinds of problems that can be encountered in the production of hybrid seed, which are better solved by the above approach than the traditional. Table 5.2 indicates the levels of seed production required to sow various levels of commercial hectarage.

If the area sown to a crop in a country is large enough to support a hybrid seed industry, a large area is required to produce this hybrid seed. The area required is usually greater than that available to a department of agriculture for seed production purposes. Of necessity, much of the seed produced must be done on privately owned land. Private incentive and private entrepreneurship obviously have a place.

Technical skills required to produce hybrid seed are rare, thus every cultivator cannot produce his own seed. Likewise the annual renewal of hybrid seed requires such large volumes that specialized equipment is necessary for handling the seed crop

Table 5.2: Seed requirements for hybrid sorghum at different levels of use on an annual basis.

Commercial hybrid area sown (ha)	Seed required (1000 kg) at 10 kg/ha sowing rate	Hybrid seed production* area required (ha)
25000	250	250
50000	500	500
100000	1000	1000
500000	5000	5000
1000000	10000	10000
5000000	50000	50000

*Assume a production of 1000 kg/ha of a hybrid seed.

from planting to sale to the ultimate consumer. To justify the expense of such equipment, large operations are necessary to insure that the cost of the equipment does not produce prohibitive increases in the cost per kilogram of seed.

A rapid expansion in production, based on targets made by the government—possibly in response to valid demands for seed—can defeat and possibly destroy the development of a seed industry. A rapidly expanded production can cause extreme shortages of seed-processing equipment. For example, a seed program designed to produce seed of new hybrids for introduction of a new concept of quality in seeds might suffer a severe setback—because hybrid seed developed under such rapid expansion would probably be produced, harvested, and processed without adequate quality control, as seed of open-pollinated varieties had been in the past. A newly developing program of certification and seed law enforcement could suffer badly or be destroyed.

A seed production industry should be developed that will meet the demand for seed—with standards set for seed of a high quality.

Responsibilities of Government

As outlined in Table 5.1, the government has obligations that can [illegible] discharged by no other groups within an eco[illegible].

Research

The government has a continuing obligation to society to maintain its leadership in adaptive research that will provide more food through still better varieties, hybrids, improved cultural practices, or improved plant protection measures.

Foundation Seed Production

Multiplication of breeder seed is required to build seed volume necessary for commercial hybrid seed production. A satisfactory foundation seed stocks organization must be developed to relieve the breeders and research workers of this reponsibility.

The fate of the entire seed industry rests on the organization that accepts responsibility for foundation seed stocks. If foundation seed supplies are limited, then the acreage of commercial plantings of that hybrid or variety will be limited. If seed stocks become impure through carelessness or negligence, then the seed producers and the consumers suffer. This function must never be allowed to become a bottleneck to the utilization of new varieties and hybrids. Quality, with all its ramifications, must be the cardinal virtue of a foundation seed program.

Foundation seed production demands special technical skills and the best lands available. Only by good fertilization on good soil will it be possible for specialists to recognize and rogue out undesirable types that frequently appear in production fields of even the best seed operations.

Quasi-governmental organizations for distribution of foundation seed develop their best working relationships when the foundation seed consumers (the commercial seed producers) become members of such organizations. The users are partially responsible for the quality of seed obtained and therefore are in a position to demand better quality seed from the foundation seed stocks organization.

Seed Certification

Seed certification is a voluntary means of preserving identity and high quality. Although the State Department of Agriculture probably could discharge this function, other agencies also might be authorized to do so. A crop or seed improvement association could be organized that would be made up of all seed producers who wanted to have a common brand name for their seed. This is often done in connection with the extension activities of an agricultural university that employs the technical staff to administer the standards developed by the association.

Seed Regulatory Work

Administration of a seed law is the proper function of government; it is the only agency that can offer adequate regulation. A flexible law should be adopted. Rules and regulations may be modified in the face of change. As seed quality is improved with the use of better equipment, more technical skill, etc., regulations could be changed to reflect this improvement. Regulations that are unnecessarily restrictive could greatly hamper the development of a seed industry. The incentives for more producer activity in the industry could be destroyed or seriously retarded. An economy that seeks a rapid rate of expansion cannot maintain restrictive and inflexible seed laws. As the industry expands and matures, the standards can be modified and raised.

Agricultural Extension

Extension workers have learned that the lower the level of education, the more intense must be the extension program to promote adoption of new practices. This is a function of the government, but must be assumed by the industry as well. Nevertheless, public-sponsored research should continue to provide new information that would be disseminated by government agencies.

Credit

Credit programs sponsored by government should be in two distinct categories: for the cultivator who is a seed consumer, and for the industry that is the seed producer. The demands for credit vary so widely that it is recommended that the two types not be administered by the same governmental or quasi-governmental agency. A single farmer, for example, might use the same type of credit for two purposes: in his role as an independent farmer, and in his role as a grower for an agent who would purchase his seed as "raw" or "rough" seed. The agent, or producer, would then assume responsibility for processing this seed and for storing the seed for future delivery; thus he would require a longer term of credit than that required for growing the crops.

The seed producer requires an entirely different type of credit than the farmer. His credit requirements might be of longer duration, because he may be required to finance the people who grow seed for him and, at the same time, to finance people who sell his seed (or in some instances, the cultivator who is a seed consumer). This credit is for his seed commodity; but in addition, he has credit requirements for capital investment and operating capital that is invested in creating useable seed from the rough or field-run seed.

Credit requirements also exist that involve foreign exchange for the purchase of specialized equipment for land shaping, seed production, seed drying and processing, and possibly for insecticides and fertilizers. Seed processing machinery is necessary for the proper maintenance of quality. Seed production equipment can increase efficiency of production. Land-shaping equipment can be used to level land to provide proper irrigation and drainage. Irrigation equipment permits more timely irrigation and more efficient use of limited supplies of water.

Targets

Programing of a growth pattern based on rates of acceptance and on normal growth rates in seed and fertilizer utilization could act as a guide to seed producers in gauging seed consumption and could serve as a production pattern.

Should total needs exceed the capabilities of production from private producers, efforts in the transition period would seek to provide incentives to produce more. A producer who has a sales outlet for the production from 100 acres, but who could produce on 500 acres, needs assurance that he would not be left holding excess supplies. A seed "bank" concept has been proposed that would enable the government to assume risks for these additional stocks so that the producer is induced to expand.

Seed Movement Restrictions

Some areas of grain production may not necessarily be the best areas for seed production. Isolation problems, weather conditions, water supply, and many other factors would determine areas for production of seed. If free movement of seed were allowed, seed producers would produce seed in the areas that are most economical for production and distribution. These locations would be used to the limit of costs of distribution. In the United States, most vegetable seed is produced in two or three western states, because climatic conditions assure producers reliable yields of high quality seed. The same is true of some legume seeds that are produced in the states of the Pacific Northwest but grown as a crop in the southeastern United States.

State line boundaries that restrict seed movement will tend to retard the development of a seed industry.

Training

A seed industry requires men with technical knowledge; training is required. This phase of a seed program can be greatly accelerated by establishing in-country training programs. Training should play a strong and important role in the development of a seed industry.

Responsibilities of Seed Producers

Table 5.1 lists the functions of the seed producer in the task of mobilizing seed growing, seed drying, seed processing, seed storage, and seed distribution. Can producers be depended upon to do this task? Will they expand to the level that will enable them to meet demands of seed production? Will they have the moral integrity to discharge this

important function in the agricultural economy? Will they produce high quality seed or will they adulterate seed and produce minimum-quality seed?

Experience has shown that—when given encouragement and entrusted with the task—seed producers can discharge these responsibilities.

They cannot be expected to assume these responsibilities if fear of changing government policy discourages substantial investments or if there is a threat of price control which could force them to sell at below-cost prices. Seed producers will prove reluctant cooperators if there is a threat of seed production on government lands that would be sold below cost of production, or if distribution of their seed is apt to be restricted to a state or part of a state.

Assuming that necessary encouragement is received from government so that private seedsmen might manage the entire industry, what would be the responsibilities of such an industry?

A seedsman who has risked his reputation in developing a seed enterprise would have his own quality control program. The seed law is not going to hamper this seedsman, because his standards would be well within the limits of reasonable laws governing quality. The law would protect him and the farmer alike from the unscrupulous practices of more unethical seedsmen who might attempt sales of seeds of the same line or hybrid that might be mislabeled as to identity, germination, purity, etc.

Seedsmen who develop a responsibility to their customers would seek better means of serving them. Thus they would be interested in better processing machinery, better seed drying and storage facilities, better distribution and merchandizing.

Efficient seedsmen would attempt to acquire more technical skills by sending personnel for training, and they would seek out people with professional training to produce better seed.

Initially seed producers might use the products of research from public institutions; later they might want to establish their own research units. They may begin by developing better varieties and hybrids for their local conditions, but in due course products from their research may be of national and international value.

Seedsmen have mutual interests in many aspects of a seed program and often form several kinds of seed organizations. The All India Seed Growers and Merchants Association and the All India Crop Improvement and Seed Producers Association are two such organizations in India. Development of a code of ethics for seedsmen; development of a liaison with governmental agencies to advise on research, seed laws, seed stock supplies, etc.; grants to research institutions to support specific research problems related to the industry—these are only a few examples of the activities that such associations might perform.

One of the greatest concerns of government is the ability to supply seed in quantity and quality to meet the needs of cultivators. It is at this point that understanding must be reached in providing a phased program that will enable the seed industry to assume these responsibilities.

Seed producers regularly overplant to assure ample supplies, regardless of weather or other hazards of production. From these excess supplies, the industry is able to maintain carryover stocks and exchange stocks in cases of local shortages due to adverse weather, etc. As production of seed develops so that higher yields per acre are obtained, the excess seed from overplanting large acreages can be reduced.

An industry that has reached maturity will be asking little from government, but will assume many risks that will be covered by profits when production is good. The mature seed industry also assumes responsibility for its carryover seed down to the retail level. All seed is returned for proper storage, retreatment, rebagging, before again being offered for sale. Unsalable seed can be used as grain to salvage some of its costs.

Experience in all phases of the seed industry has been gained by a number of seed enterprises in Europe and the USA. Some of these companies are currently sharing these skills in developing similar industries in South America and Africa.

APPENDIX 1

Appendix 1 is composed of adaptations of papers by the following authors—Johnson E. Douglas ("The Seed Law," "Guidelines for Establishing a Seed Certification Agency," and "Seed Policy"), L.R. House ("A Variety Release Committee"), and Wayne H. Freeman and Johnson E. Douglas ("A Foundation Seed Stocks Agency").

The Seed Law

For an effective seed industry to develop that can provide seeds of high quality to cultivators at reasonable prices, there must be seed laws requiring minimum standards of germination, purity, weed-seed content, and other seed qualities. The seed law must specify the information required on the label when seed is sold and must insure that such information is accurate. Furthermore, provisions must be made for the enforcement of the seed law. A Seed Committee, central and/or state, can be organized to interpret and modify the law as conditions change.

Given such a compulsory seed control system, properly enforced, cultivators can be assured of obtaining a seed of known kind and quality. Further, the legitimate seed industry can flourish without unfair competition from unscrupulous operators.

Effective seed control requires: (1) a seed law and seed law enforcement in each state for seed produced and marketed in that state; and/or (2) a national seed law and seed law enforcing agency to control seed that moves in interstate commerce. To avoid unnecessary confusion, the seed laws in the several states would be as uniform as possible. The steps required to accomplish these objectives are listed below.

Development of a Model Seed Law

The Director of Seed Production and Distribution should develop a model seed law applicable to a country's conditions and legal requirements after:

- Consulting with crop botanists, plant breeders, extension personnel, seed producers, members of existing seed firms, and other agricultural officials regarding:

  -terminology and definitions to be used in the model seed law,

  -specification regarding amounts of other crop seeds and various kinds of weed seeds that will be permitted,

  -kind of seed labeling to be required,

  -other technical provisions of the model seed law; and

- Consulting with appropriate legal advisors the wording of the model seed law.

Adoption of Seed Laws: To establish state seed laws the Director of Seed Production and Distribution should work with appropriate officials in each state to insure that its seed law is drafted from the model. In the state seed law, or in supplementary, parallel legislation, provision must be made for establishing a Seed Law Enforcement Agency under the Director of Agriculture.

To develop a draft of a national seed law to be submitted to the Parliament for enactment, the Director of Seed Production and Distribution should work with appropriate officials of the Central Government. In the national seed law, or in supple-

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mentary, parallel legislation, provision must also be made for establishing a Seed Law Enforcement Agency, under an appropriate official of the Ministry of Food and Agriculture.

Seed Law Enforcement Agency

The Director of Seed Production and Distribution should consult the appropriate officials in setting up and selecting personnel for the seed law enforcement agency in each state, which should be separate from the states' extension and research organizations. In each state, the agency should consist of the following:

Seed Law Enforcement Officer: This official should have training and experience in laboratory work, as well as postgraduate training or equivalent experience in economic botany. His responsibilities are to be in charge of the state seed testing laboratory, supervision of inspectors collecting official samples, issuing necessary information regarding the seed law, issuing regulations required in administration of the seed law, and taking such action as required for enforcement of provisions of the seed law.

Official Seed Board

This Board should hear and act upon appeals of decisions and actions of the Seed Law Enforcement Officer, approve regulations formulated by him, and advise him in law enforcement procedures. The Board should have the Director of Agriculture as Chairman and three representatives of the seed industry (corporations, cooperatives, or private companies engaged in merchandising seed), in addition to three representatives of farmers, preferably nominated by the farmers' forum, and one representative each of extension and plant breeding research.

Official Seed Testing Laboratory

Staff (in addition to the Seed Law Enforcement Officer who will be the officer in charge): Chief Seed Analyst, Laboratory Assistant, such additional seed analysts, laboratory assistants; and clerical help as required by the volume of testing work.

Functions: Test all official samples drawn by Inspectors in routine inspections and in cases involving litigation. Provide testing (on a fee basis) of samples submitted by seed producers, seed merchants, cultivators, and others. Complete analysis of samples submitted for certification until such time as the volume of official seed testing and of seed certification warrants the establishment of a separate laboratory for the latter service.

Facilities: Building space, including offices for staff and records, and a seed laboratory. Laboratory equipment and people trained to use it.

Official Inspectors

Duties: To draw official samples on a spot-checking basis of seed moving in market channels or offered for sale in seed stores. To draw official samples upon request of the owner of seed, or in cases involving legal action, to serve as agents of the Seed Law Enforcement Officer in carrying out acts of seed law enforcement and in gathering information necessary for enforcement.

Number of Inspectors: Ultimately, there will probably be need for an average of one Inspector in each district. Initially one inspector should be provided for each district in which special emphasis is being given to an improved seed program; for example, districts in which certified seed corporations or cooperatives are established.

In addition to simple sampling equipment, such as bag probes, scopes, buckets, and sample bags, each Inspector will require a vehicle (such as a jeep) for adequate service within his assigned area.

Financial Requirements

Salaries and travel expenses would be required for staff, which might include the following for a state or region:

Seed Law Enforcement Officer
Chief Seed Analyst
Laboratory Assistant
Three to five Inspectors
Clerical help as required

Equipment and Supplies:

Building and seed laboratory equipment
Supplies of germination paper, bags, labels, office supplies, etc.,
Three to five motor vehicles.

Guidelines for Establishing A Seed Certification Agency

Seed Certification Agencies established by the various provinces, districts, and states seek to maintain

and multiply high-quality seeds of superior varieties of crops, grown and distributed so as to insure genetic identity and purity.

The certification agency established under the Seed Act might be an association incorporated under the laws of the country as a nonprofit (not for profit) corporation whose principal objective is to conduct seed certification.

The certification agency created would be a legal entity operating as an independent agency reporting to the Government.

The Seed Certification Agency would not be engaged in the production, processing, or the distribution of seeds as an agency or corporation. However, the Seed Certification Committee (which should be the governing body of the established Seed Certification Agency) could be composed, in part, of persons engaged in such production, processing, and distribution of seed.

Members of the Seed Certification Committee may be appointed by the Government and could be composed of persons in the following categories.

No. of Representatives	Interests Represented
2	Plant Breeders
1	Plant Pathologists
2	Certified Seed Producers
2	Seed Dealers of Certified Seed
1	Secretary of Agriculture
1	Agricultural Extension Service
1	Agricultural University
1	Deputy Director of Agriculture (Seed)
1 (ex officio)	The Seed Certification Officer
1 (ex officio)	The Chief Seed Analyst
1 (ex officio)	Chief Seed Inspector
1 (ex officio)	Liaison Representative of the Central Government

The Seed Certification Officer might serve as Secretary of the Committee.

Persons appointed to the Seed Certification Committee by the Government at the outset (other than those serving in ex-officio capacity) should be appointed for 1-year or 2-year terms so that persons representing special interests shall serve staggered terms. Thereafter, appointment should be for 2-year terms so as to provide continuity of membership on the Committee. After serving on the Committee a person may be reappointed to the Committee.

When an organization of certified seed *producers* attains a paid-up membership of 25 or more bonafide members, the Secretary of Agriculture could be notified. Thereafter, the organization of certified seed producers might nominate three of their members for appointment to the Committee and the Government could appoint two of those nominated at the outset, and one thereafter.

Similarly, when an organization of seed *dealers* who distribute certified seed attains a paid-up membership of 25 or more bonafide members, the Government could be notified. Thereafter, this organization of certified seed dealers could nominate three of their members for appointment to the Committee, and the Secretary of Agriculture could appoint two from those nominated at the outset, and one thereafter.

When an organization is developed that adequately represents both certified seed producers and dealers of certified seed, the organization could nominate ten persons, three of whom should be certified seed producers and three of whom should be dealers in certified seed. Upon receipt of these nominations, the Government could appoint two seed producers and two seed dealers to the Seed Certification Committee at the outset, and one thereafter.

If more than one organization of certified seed producers or of certified seed dealers qualifies as above, each could submit nominations for consideration by the Government in making appointments.

Fees collected for inspections would be placed in a revolving fund under the control of the certifying agency, and would be expended by the certification committee on proper vouchers to meet all necessary expenses (including salaries of necessary staff; procurement of necessary vehicles, equipment, and supplies; paying necessary travel expense of officers, inspectors, and committee members; and expense of publications). Reports of receipts and expenditures should be made to the Government as prescribed.

Functions of the Seed Certification Agency

1. Verify varietal purity and identity of seed varieties released for certification, and verify that the certified seed producer receives and plants such seed under prescribed conditions.
2. Outline procedures for the production, harvesting, processing, storage, and labeling of seeds intended for certification so that seed lots finally approved for certification are true to variety and meet minimum standards for certification.

   Provide applications and other necessary

forms, together with information on standards and procedures for certification to all persons having the requisite qualifications and who show interest in certified seed production.

Verify upon receipt of an application for certification that the variety is eligible for certification, that the seed source used for planting was authenticated by certification tags and records of purchase in accordance with rules prescribed, and that the prescribed fees were submitted with the application.

3. Inspect fields to assure that the prescribed minimum standards for isolation, planting ratio, roguing (where applicable), use of male-sterility (where applicable), and similar factors are maintained at all times, as well as to insure that seed-borne diseases are not present in the field to a greater extent than provided in the prescribed standards for individual crops. The presence and rate of occurrence of prohibited, restricted, and other objectionable weed seeds shall appear in the field inspection report.

   Decide by majority vote of the Committee (under procedural rules adopted by the Committee) whether each lot of seed produced under its jurisdiction meets all prescribed requirements for certification. Such decisions for each lot of seed may be delegated to the Seed Certification Officer in those cases where compliance is obvious, but would always be subject to review by the Seed Certification Committee.
4. Sample and inspect seed lots produced under the procedures prescribed by the certification agency and submit such samples to the State Seed Laboratory for testing to assure that the seed meets prescribed seed quality and germination standards.
5. Inspect seed processing plants to see that admixtures of other kinds and varieties are not introduced, that the processing is conducted in such a way as not to injure the seed, and that such processing results in high quality seeds as prescribed in the standards.
6. Develop a list of seed processing plants with personnel and equipment capable of meeting the objectives stated in paragraphs above; designate such plants as "approved processing plants" for processing certified seed and provide a suitable emblem to identify such approved processing plants; and withdraw approval and the the emblem if the processing plant fails to maintain prescribed standards.
7. Develop in consultation with the Central Seed Committee the form of certification tags to be used for identifying the various lots and generations of certified seed, and issue such tags.
8. Assure that the field inspections required to maintain the purity of the variety are thorough and timely; that inspection of seed lots produced under the supervision of the Seed Certification Agency are timely; that such samples are promptly submitted to the seed analyst having jurisdiction; and that certification, tags, labels, and seals are issued expeditiously so that orderly marketing of the seed is possible.
9. Conduct educational programs designed to promote the use of the certified seed, including a publication listing certified seed growers and sources of certified seed.
10. Charge such fees as may be necessary to meet all costs incurred in carrying out the duties and responsibilities of the certification agency after a preliminary grant is made by the Government to start the program.
11. Employ such staff as is necessary to carry out the prescribed function, including:
    A Seed Certification Officer,
    Seed Certification Inspectors as needed,
    Adequate clerical staff.

    Acquire office and storage space, together with the equipment and supply forms necessary for operating the program efficiently.
12. Make provisions for the travel necessary to provide timely field and seed inspections.
13. Cooperate fully with all persons, public and private, in matters relating to seed improvement in the country.
14. Operate through a Seed Certification Committee, which shall be the governing body of the seed certifying agency and which shall represent official, technical, seed producer, and seed dealer interests. The Committee shall elect officers and adopt by-laws, and may appoint such subcommittees as may be necessary to give attention to problems relating to specific crops and to other specific problems as they arise.
15. Adhere to minimum standards for certification prescribed by the Government on the advice of the Central Seed Committee.
16. Operate so as to insure a close working relationship between certified seed growers, certified seed dealers, agronomy research personnel, Agricultural Universities, and Regional Departments of Agriculture, together with seed analysts and seed inspectors appointed under the Act.

17. Maintain records necessary to verify that seed planted for the production of certified seed is eligible for such planting under these rules.
18. Set up procedures for handling appeals.
19. Vigorously investigate violations and apparent violations of the Seed Act as it pertains to certified seed, and take appropriate action. Use of the words "Foundation," "Registered," "Certified" in connection with seed that has not been certified as prescribed would be an offense and a violation of the Seed Act. Likewise, attachment of certification tags to seed that is not certified seed as defined is an offense and a violation of the Act.
20. Outline the duties of Seed Certification Officers, Inspectors, and other personnel employed by the agency.

Long-Term Seed Policy

A good quality seed production program for high-yielding varieties and hybrids requires the strongest possible support and encouragement. However, in the enthusiasm to move ahead rapidly, thought must continually be given to the long-term objectives, to how these objectives can be achieved, and to the probable effect of current actions.

The thousands of acres of seed production ultimately needed to supply cultivators with hybrid seed and seed of improved varieties requires the contributions of hundreds of people and organizations. It is recognized that government agencies cannot perform this tremendous task alone. They need the help and support of private seed producers; their active interest and participation in seed production, processing, and marketing is vital to a dynamic seed production and distribution program.

Therefore, it is important to formulate policies that provide opportunities for organizations and individuals to make their maximum contribution. A review of the roles to be played by both the public and private sectors of the seed program can suggest policies that will assist in delineating those functions.

Major Responsibilities of the Central Government

1. Encourage and offer financial support to the Crop Improvement Programs (Research).
2. Create and promptly implement rules and regulations under the Seed Act.
3. Support the production of foundation seeds of hybrids through the recognized Foundation Seed Stocks Agency (but at the same time recognize the need and opportunities for others to do likewise).
4. Assist in the development of a seed industry through the encouragement of private individuals, cooperatives, and corporations. Assistance for these organizations might include:
   - Special credit
   - Assistance in the evaluation of equipment for seed processing
   - Market development and salesmanship guidance
   - Land development and irrigation
   - Sharing of germplasm in the breeding programs

Major Responsibilities of the District, Province, or State Governments

1. Strengthen breeding efforts in their area.
2. Establish a Seed Certification Agency in cooperation with the Agricultural University and seed producers in the region to implement a seed certification program.
3. Develop a small well-qualified and trained staff for seed sampling and enforcement of the truthful labeling provision of the Seed Act.
4. Establish a strong seed testing laboratory in the region to meet the requirements of the certification and seed law enforcement programs.
5. Locate and train seed producers.
6. Develop an extension staff capable of effective technical guidance in seed improvement.

Role to be Played by the Seed Industry

1. Arrange for the production, processing, and distribution of seeds of hybrids and lines: these organizations should develop markets for their seeds; some government purchase may be helpful initially to help assume risk, but this should be quickly phased out.
2. In instances where these organizations can contribute to the development of hybrids and lines available to the cultivators, they should be encouraged in their breeding efforts and in foundation seed production.
3. Participate in the Central Seed Committee and similar district committees in drafting policies for the seed program.
4. Build necessary facilities such as seed processing plants and warehouses and develop land resources for maximum good quality seed production.

Policies designed to assist in the development of a strong seed industry should include:

1. Opportunity for all to market certified or noncertified seeds in a competitive manner under the Seed Act at prices that are remunerative and competitive.
2. Encouragement in the development of strong breeding programs in both the public and private sectors.
3. Arrangements to certify both publicly and privately developed hybrids and varieties.
4. Opportunities to sell privately and publicly developed hybrids after a simple declaration of intent to do so. Sales of seeds of these hybrids would be in accordance with the seed law, and possibly could be certified.
5. Support of collaborative arrangements with seed firms outside the country so that their technical expertise will be available to the country.
6. Regulations that prevent establishment of a monopoly by either public or private organizations.
7. Provision of an easily accessible source of credit for seed production, processing, and distribution organizations to meet their special needs for large amounts of money during certain periods.
8. Availability of germplasm from the breeding material of the research programs to any interested citizen or organization.

The Variety Release Committee

The purpose of a formal cultivar release is to review data supporting a new hybrid or line, to determine its uniqueness and place for the farmer. The Variety Release Committee can be made up of scientists, men from the industry, and administrators, each capable of judging merits of a new candidate but not involved with its development. The originating breeder or appropriate individual may defend the release to the committee. The functions of the Variety Release Committee are to:

1. Be responsible for the release of hybrids and lines developed by governmental institutions and other public agencies (Agricultural Universities). The determination to release would be based on merit and uniqueness—what does the cultivar contribute that is not provided by an existing line or hybrid? These advantages might be adaptation to a different area, disease resistance, improved grain quality etc., as well as yield. This is a mechanism to restrict a number of very similar types from reaching the market.
2. Provide proforma for applying for the release of a line or hybrid. Release usually depends not only on distinctness, but on the availability of a reasonable quantity of breeders' seeds (10 to 20 kg), or seed of the parents of a hybrid.
3. Determine responsibility for the maintenance of breeders' seed. This is usually the responsibility of the originating breeder or institution.
4. Make formal notification that the line or hybrid has been released. This formal statement indicates that the foundation seeds stocks agency can produce foundation seed (it will usually produce a modest amount of seed in anticipation of release so that sample lots can be provided to producers). It also signals to the certification agency that the cultivar is suitable for production in the certification program.
5. Provide the seed certification program with descriptive information regarding the morphological characteristics of released lines and parents of hybrids. This is to enable the certification agent to identify rogues in production fields.
6. Remove obsolete lines and hybrids from the list of those eligible for seed certification.
7. Issue a short statement to the press and/or publish a short article about the release, properly assigning credit to the individuals and institutions responsible for the development of the newly released line or hybrid.

The Foundation Seed Stocks Agency

Initially, a Foundation Seed Stocks Agency, established as a semigovernment operation might undertake a number of functions to help get a seed program moving. It would seek to:

1. Maintain an aggressive and high-quality foundation seed program.
2. Develop a service branch that would provide services in seed plant construction and operation and land development for irrigation and drainage. Frequently, knowledgeable sources for such services are not available and would be a major contribution to a developing seed industry. This service could expedite development by providing specifications for equipment; by creating demands for construction machinery and supplies; by acting as factory representatives to bring manufacturers in contact with customers; by

helping maintain standards of production by providing a consulting service for customers; and by providing sound advice on design and construction of plants. A consulting service that could help seed producers determine how best to organize irrigation and drainage of their farms would be a tremendous contribution. This service could help them determine the irrigation systems most effective for their needs, the necessary equipment and cost inputs, and the companies and sources that could do the work and supply the items.

3. Act as a manufacturer's representative, possibly on a commission basis, for the sale of seed production and processing equipment and materials. Provide guidance to such manufacturers regarding kinds of equipment needed and quality desired.
4. Develop a market advisory service that would bring buyer and seller together and assist organizations in building their distribution and sales programs.
5. Conduct training programs for seed production and processing. The numerous topics that might be included in such a training program are listed below (from training manuals by the National Seeds Corporation, written for use in training programs in India). Note that many practical training periods have also been provided to teach adjustment of farm machinery and processing equipment and calibration of sprayers, etc. Training should include an overseas experience for selected key individuals and study awards for promising young people.

Topics that might be included in a training program:

Review of plant breeding research on crops relevant to the seed production program; Land shaping and smoothing; Tractor-powered equipment for land shaping and for development of surface irrigation; A guide to application of irrigation waters; Measuring irrigation water; Systems of irrigation—furrow, border strip, sprinkler, etc; Plant nutrition and determination of fertilizer needs; Soils and plant nutrition; Major fertilizer elements; Diagnosis of nutrient deficiencies in plants; Operation and maintenance of various types of planters; Cultivation and weed control; Plant protection—insect and disease control on crops in the production program; Control of rodents; Toxicity to mammals of insecticides and fumigants; Building a quality seed industry; Viability, vigor, and dormancy in seeds; Seed maturation; Production techniques for crops in the production program; Some aspects of applied physiology—moisture, temperature, floral initiation; How to become a seed producer; Developing a comprehensive seed certification program; Development and operation of a seed certification agency, Application for certification; The seed certification Inspector; Certification standards for the various crops in the production program; Handling and completing inspection reports; Field mapping; Method of inspecting fields; Seed Act and the cultivator; Seed testing; Seed vigor and vigor tests; Minimum certification standards for the crops in the production program; Cultivar identification—ability to determine off-type plants; Mechanical threshing; Uniform handling for conditioning harvested crops; Harvesting and drying; Principles of seed separation—physical characteristics utilized in seed cleaning and sizing; Seed cleaning, sizing, and separation with various types of machines; Seed treatment—precautions in the use of fungicides and insecticides in the treatment of seeds; Use of a slurry seed treater; Seed treatment recommendations; Seed conveyors; Bag-closing machines; Mechanical injury to seeds—its causes and effects; Seed processing facility; Practical solutions to seed storage problems; Drying, storing, and packaging seeds to maintain germination and vigor; Economics of seed production, processing, and distribution; Public relations; Salesmanship, publicity; Self regulation in business; Establishing arrangements for helping to finance seed enterprises.

The functions of such a Foundation Seed Stock Agency are countrywide. It is important that there be close liaison between central office and field staff; direct field contact through visits from the central office will help.

The operation of periodic in-service training functions and seminars will help keep older staff members up to date.

The provision of adequate mobility and effective field support is a must if the job is to be effectively accomplished.

Even though a Foundation Seed Stocks Agency is established initially to help get a seed program moving, the production of foundation seed by other agencies, both public and private, should be encouraged and assisted. Private companies that eventually undertake their own research will want to manage the production of their own foundation seed. The burden of producing foundation seed

might become great enough that the operation of foundation seed units in various districts, provinces, states, etc., may be desirable. No one agency should have a monopoly on the production of foundation seed for the long-term good of the seed industry.

At times, the local production of seed may exceed local demand, or there may be a crop failure because of weather conditions, etc., in one portion of the country. A clearing house to help get seed moved from a surplus to a shortage area would be very helpful. Seed should not be subject to the same regulations as grain if such regulations exist.

The provision of a market development consulting service may be useful in helping growers organize independent production/marketing organizations.

Clearly, many services are required that could be initiated by a Foundation Seed Stocks Agency in the interest of getting a good seed production program going. Many of these suggested functions could eventually be assumed by other agencies or companies (such as land development), and this process could be encouraged.

APPENDIX 2

Sorghum Descriptors

An effort has been made by sorghum scientists working with the International Board for Plant Genetic Resources (IBPGR) to identify descriptive and economic traits useful to describe entries in the world collection. The following list has been organized; in many instances, the information is also useful to a breeder taking notes in his nursery or yield trials.

1. Accession Identifier

1.1. IS number:	Every accession in the sorghum germplasm bank will be identified by its IS number (IS = International Sorghum)
1.2. Other number:	This is the number assigned by other institutes of different countries, viz. PI number, MN number, E number, EC number, etc.
1.3. Source of supply:	The name of the donor institute and country from which the material was supplied.
1.4. Type of accession:	Ao = Authentic indigenous collection - unselected landrace (original seed) An = Authentic indigenous collection - unselected landrace (seed increased "n" times) EL = Experimental accession (selected landrace) EB = Experimental accession (Breeders' line) UN = Unknown
1.5. Local name/pedigree:	If Ao or An, local name; EL or Eb, pedigree
1.6. Name(s) of the bank:	Name(s) of the germplasm Bank(s) where the accession is stored

2. Field Collection Data

2.1. Collection number:	Three-letter abbreviation of the collector's name, followed by a number up to five digits. Example: KEP 00332
2.2. Date of collection:	The date on which a particular accession was collected, expressed numerically as month and year in four digits. Example: July 1977 = 0777
2.3. Country:	An abbreviation for the country of origin, using United Nations abbreviations.
2.4. Province:	Name of the territorial subdivision of the country.
2.5. Precise locality:	Direction and number of kilometers from the village or specific known area on the road map Example: 25N Babati
2.6. Latitude:	Latitude in degrees (2 digits) and minutes (2 digits) with suffix N or S.

2.7. Longitude:	Longitude in degrees (3 digits) and minutes (2 digits) with suffix E or W.
2.8. Altitude:	Elevation above sea level expressed in meters, up to four digits.
2.9. Climatic code: (Troll's climatic classification):	Troll classified the tropical climates on the basis of broad rainfall groups in relation to potential evapotranspiration. V1 = Tropical rainy climates with rainy season of 12 to 9½ humid months, with short interruptions. Evergreen tropical rainforests and half-deciduous transition wood. V2 = Tropical humid-summer climates with 9½ to 7 humid months; raingreen forests and humid grass-savannah. V2a = Tropical winter-humid climates with 9½ to 7 humid months; half-deciduous transition wood. V3 = Wet-dry tropical climates with 7 to 4½ humid months; raingreen dry wood and dry savannah. V4 = Tropical dry climates with 4½ to 2 humid months: Tropical thorn-succulent wood and savannah. V4a = Tropical dry climates with humid months in winter. V5 = Tropical semi-desert and desert climates with less than 2 humid months: Tropical semi-desert and deserts. (A humid month is defined as a month with mean rainfall exceeding potential evapotranspiration)
2.10. Climatic code (rainfall):	1 = Less than 450 mm 2 = 450-650 mm 3 = 650-900 mm 4 = Above 900 mm
2.11. Climatic code (rainfall distribution):	1 = Uniform 2 = unimodal 3 = bimodal
2.12. Climatic code (rainfall assured or erratic):	A = Assured E = Erratic
2.13. Cultural practice:	D = Dry land I = Irrigated F = Flooded T = Transplanted
2.14. Sample source:	F = Field collection S = Farmer's seed sample M = Market sample
2.15. Ethnic group:	Name of tribe or ethnic group living in the area where a particular germplasm accession was collected, if applicable.

3. Taxonomic and Morphological Evaluation Data

3.1. Classification:	B = Bicolor G = Guinea C = Caudatum

K = Kafir
D = Durra
GB = Guinea Bicolor
CB = Caudatum Bicolor
KB = Kafir Bicolor
DB = Durra Bicolor
GC = Guinea Caudatum
GK = Guinea Kafir
GD = Guinea Durra
KC = Kafir Caudatum
DC = Durra Caudatum
KD = Kafir Durra
AR = Arundinaceum
VG = Virgatum
VE = Verticilliflorum
AE = Aethiopicum
PQ = Propinquum
SH = Shattercane
TW = Tetraploid Wild
AN = Anomalous

3.2. Group name:

Rx = Roxburghii
Sh = Shallu
Ka = Kaoliang
Br = Broomcorn
Ft = Feterita
Ng = Nigricans
Do = Dobbs
Kr = Kaura
Zr = Zera-Zera
Nd = Nandyal
Md = Maldandi
Ml = Milo
Sg = Sudangrass
Mb = Membranaceum
Kf = Kafir
Hg = Hegari
Dr = Durra
Wn = Wani
Ca = Cane
Gg = Grain grass
Pg = Patcha jonna (Yellow pericarp jowars)
Fr = Fara-Fara

(It is recognized that this list is incomplete and can be augmented time to time)

3.3. Shattering:

CS = Completely shattering
MS = Moderately shattering
NS = Nonshattering

3.4. Plant color:

P = Pigmented
T = Tan

3.5. Stalk juiciness:

J = Juicy
D = Dry

3.6. Stalk sweetness:	S = Sweet I = Insipid
3.7. Midrib color:	C = Colorless (white) D = Dull green Y = Yellow B = Brown
3.8. Ear compactness and shape (Fig. A2.1):	1 = Very lax panicle typical of wild sorghums 2E = Very loose erect primary branches 2D = Very loose drooping primary branches 3E = Loose erect primary branches 3D = Locse drooping primary branches 4E = Semi-loose erect primary branches 4D = Semi-loose drooping primary branches 5 = Semi-compact elliptic 6 = Compact elliptic 7 = Compact oval 8 = Half broomcorn 9 = Broomcorn
3.9. Glume color:	W = white S = Sienna (yellow) M = Mahogany (brown) R = Red P = Purple B = Black G = Grey
3.10. Kernel covering (Fig. A2.2):	1 = Grain uncovered 2 = ¼ grain covered 3 = ½ grain covered 4 = ¾ grain covered 5 = Grain fully covered
3.11. Awning (at maturity):	A = Awned L = Awnless
3.12. Kernel color:	1 = White 2 = Yellow 3 = Red 4 = Brown 5 = Buff
3.13. Weight of 100 kernels:	Weight of 100 kernels in grams at moisture content equal to or less than 12%.
3.14. Endosperm texture (Fig. A2.3):	1 = Completely corneous 2 = Almost corneous 3 = Partly corneous 4 = Almost starchy 5 = Completely starchy
3.15. Endosperm color:	W = White Y = Yellow
3.16. Kernel luster:	L = Lustrous N = Nonlustrous

3.17. Presence of subcoat:	P = Present A = Absent
3.18. Kernel form (Plumpness, Fig. A2.4):	D = Dimple P = Plump
3.19. Seed form (Twinning, Fig. A2.5):	T = Twin S = Single

4. Agronomic Evaluation Data

4.1. Place of evaluation:	Place of the Research Institute abbreviated
4.2. Date of planting:	Day month year (2 digits each)
4.3. Early seedling vigor:	Recorded at 15 days after emergence — 1 = Very good 2 = Good 3 = Average 4 = Below average 5 = Poor
4.4. Plant height (Fig. A2.6):	Measure the average height of the row in cm from the base to the tip of the ear before harvest and after 50% flowering.
4.5. Days to 50% flowering:	Number of days from mean emergence date of the field to the date when 50% of the plants in the plot started flowering.
4.6. Photosensitivity:	I = Insensitive M = Medium sensitive S = Highly sensitive (Recorded later on the basis of *kharif/rabi* ratios of plant height and days to 50% flowering. *Kharif* is the summer season, the season with longer day lengths; *rabi* is the winter season, the season of shorter day lengths.)
4.7. Mean number of effective tillers:	Average number of heading stems from 10 representative plants (Main stem considered as tiller 1).
4.8. Synchrony of flowering (Main stem and tillers flower at the same time):	S = Synchronous N = Nonsynchronous
4.9. Peduncle exsertion and recurving (Fig. A2.7):	1 = Well exserted more than 10 cm between ligule of the flag and ear base 2 = Exsertion 2 cm to 10 cm between ligule of flag leaf and ear base 3 = Less than 2 cm, but ligule definitely below the panicle base 4 = Peduncle recurved, but panicle is below the ligule and clearly exposed, splitting the leaf sheath 5 = Ear covered by the leaf sheath
4.10. Head length:	Length from the base of the ear to the tip in centimeters
4.11. Head width:	Width in natural position at the widest part of the ear in centimeters
4.12. Threshability:	1 = Freely threshable (0-10% unthreshed kernel) 2 = Partly threshable (10-50% unthreshed kernel) 3 = Difficult to thresh (More than 50% unthreshed kernel)

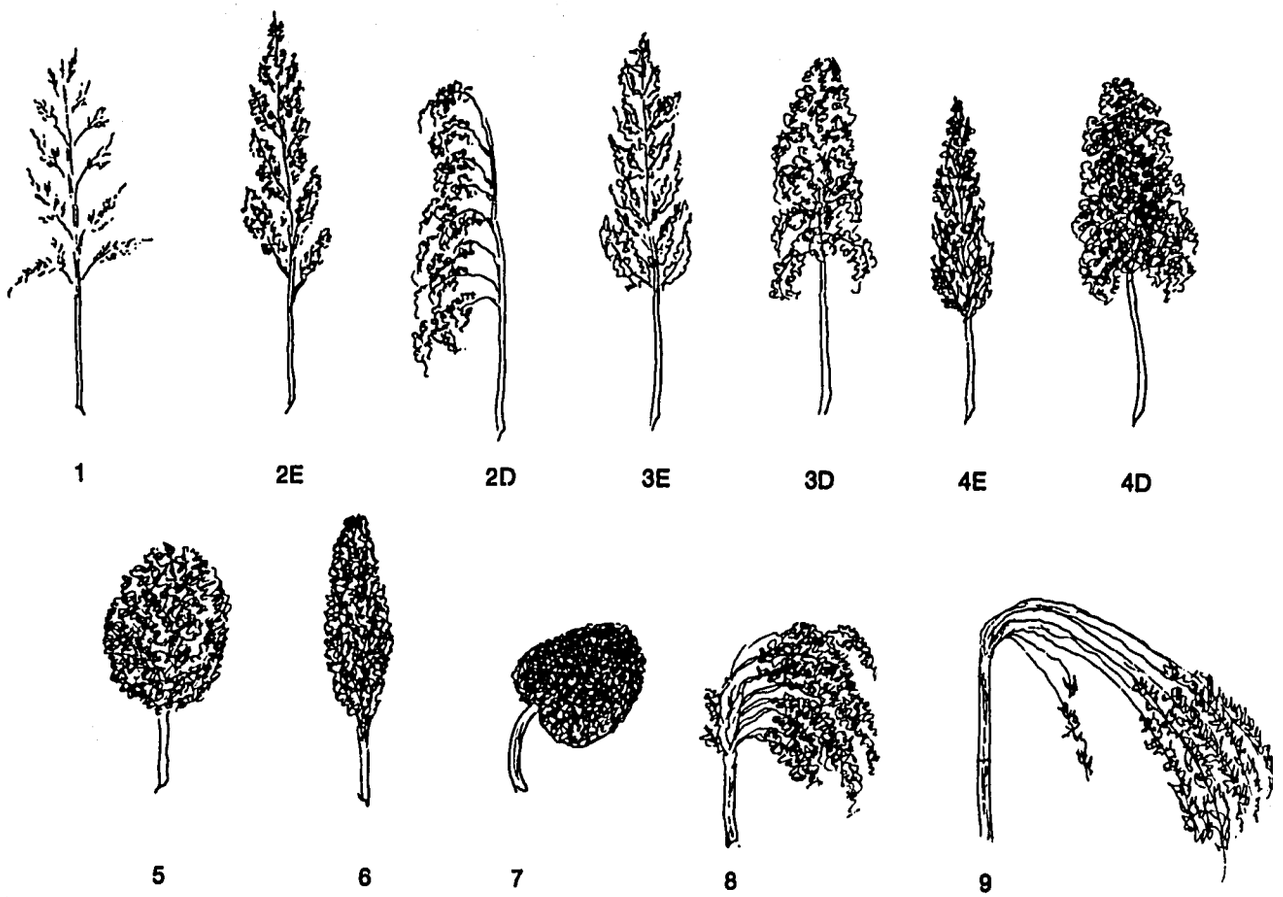

Figure A2.1: Ear compactness and shape.

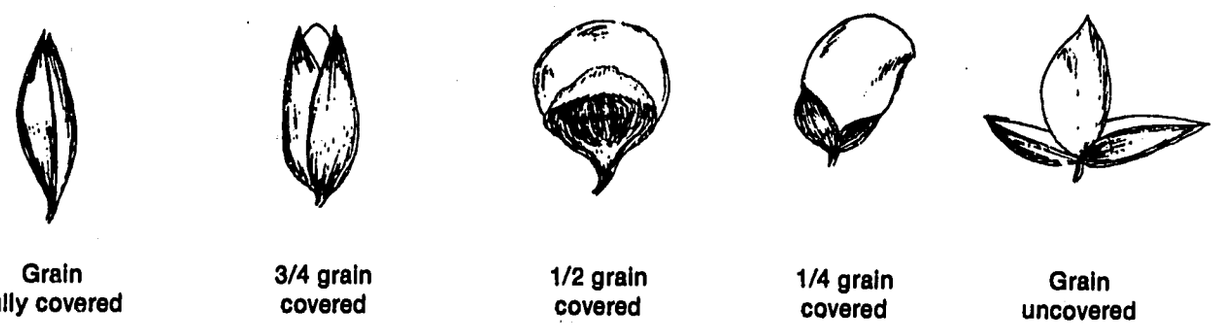

Figure A2.2: Kernel covering.

Figure A2.3:Endosperm texture.

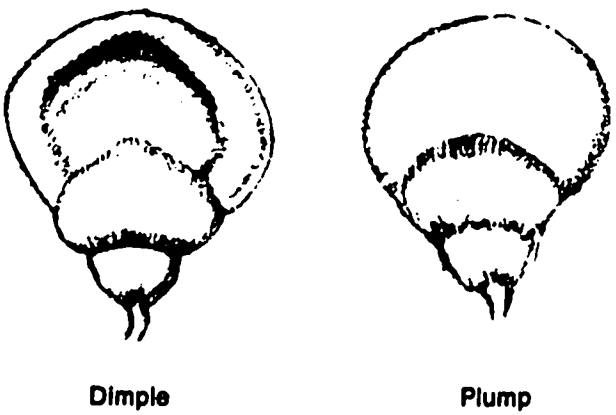

Figure A2.4:Kernel form.

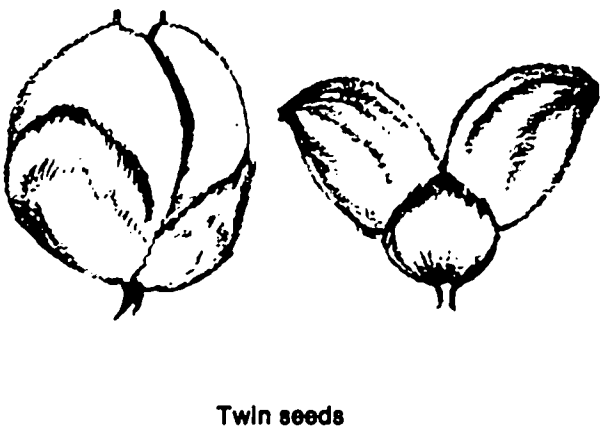

Figure A2.5:Seed form.

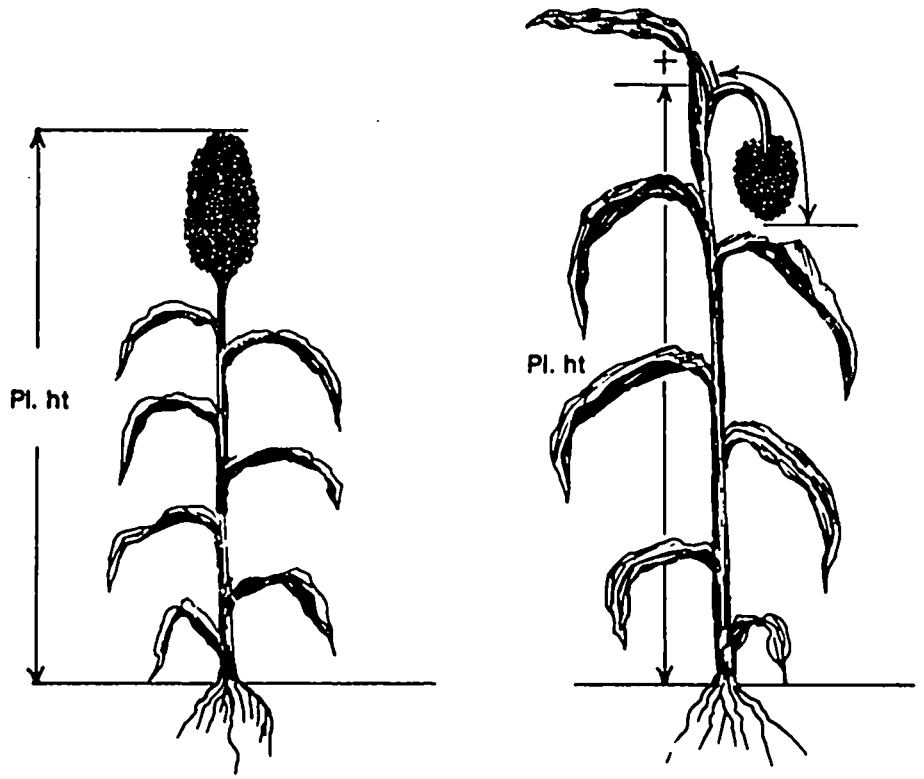

Figure A2.6:Plant height.

Figure A2.7: Peduncle exsertion and recurving.

4.13. Kernel hardness: Weight in kilograms required to crack the grain

4.14. Lodging:
1 = 10% of the plants lodged
2 = 10-25% of the plants lodged
3 = 25-50% of the plants lodged
4 = 50-75% of the plants lodged
5 = 75-100% of the plants lodged

4.15. Weathering ability:
1 = Very good
2 = Good
3 = Average
4 = Below average
5 = Poor

4.16. Overall plant aspect:
1 = Very good
2 = Good
3 = Average
4 = Below average
5 = Poor

5. Pest Resistance Evaluation Data

Score recorded under this category will be suffixed by N or A to indicate N = Natural infestation, A = Artificial infestation.

Shoot or stem fly:

5.1. *Atherigona soccata* (Rondani)

5.1.1. Deadhearts at 28 days:
1 = None
2 = 1-10%
3 = 11-25%
4 = 26-40%
5 = More than 40%

Stem borers:

5.2. *Chilo partellus* (Swinhoe)

5.2.1. Damage at 5 weeks:
1 = No leaf damage
2 = 1-10% of plants with one or more leaves damaged
3 = 11-25% of plants with one or more leaves damaged
4 = 26-40% of plants with one or more leaves damaged
5 = More than 40% of plants with one or more leaves damaged

5.2.2. Deadhearts at 7 weeks:
1 = None
2 = 1-10%
3 = 11-25%
4 = 26-40%
5 = More than 40%

5.2.3. Tunneling at harvest:
1 = None
2 = Confined to 1 node
3 = One node crossed
4 = Two or three nodes crossed
5 = Four or more nodes crossed

5.3. *Busseola fusca* (Fuller)

5.3.1. Damage at 5 weeks: 1 = No leaf damage

2 = 1-10% of plants with one or more leaves damaged
3 = 11-25% of plants with one or more leaves damaged
4 = 26-40% of plants with one or more leaves damaged
5 = More than 40% of plants with one or more leaved damaged

5.3.2. Deadhearts at 7 weeks:
1 = None
2 = 1-10%
3 = 11-25%
4 = 26-40%
5 = More than 40%

5.3.3. Tunneling at harvest:
1 = None
2 = Confined to 1 node
3 = One node crossed
4 = Two or three nodes crossed
5 = Four or more nodes crossed

5.4. *Sesamia cretica* (Led.)

5.4.1. Damage at 5 weeks:
1 = No leaf damage
2 = 1-10% of plants with one or more leaves damaged
3 = 11-25% of plants with one or more leaves damaged
4 = 26-40% of plants with one or more leaves damaged
5 = More than 40% of plants with one or more leaves damaged

5.4.2. Deadhearts at 7 weeks:
1 = None
2 = 1-10%
3 = 11-25%
4 = 26-40%
5 = More than 40%

5.4.3. Tunneling at harvest:
1 = None
2 = Confined to 1 node
3 = One node crossed
4 = Two or three nodes crossed
5 = Four or more nodes crossed

5.5. *Diatraea saccharalis* (Fabricius)

5.5.1. Damage at 5 weeks:
1 = No leaf damage
2 = 1-10% of plants with one or more leaves damaged
3 = 11-25% of plants with one or more leaves damaged
4 = 26-40% of plants with one or more leaves damaged
5 = More than 40% of plants with one or more leaves damaged

5.5.2. Deadhearts at 7 weeks:
1 = None
2 = 1-10%
3 = 11-25%
4 = 26-40%
5 = More than 40%

5.5.3. Tunneling at harvest:
1 = None
2 = Confined to 1 node
3 = One node crossed
4 = Two or three nodes crossed
5 = Four or more nodes crossed

5.6. Other stem borers: Score 1-5

Head feeders:

5.7. Midge, *Contarinia sorghicola* (Coquiller):	1 = No damaged grain 2 = 1-10% damaged grain 3 = 11-25% damaged grain 4 = 26-40% damaged grain 5 = More than 40% damaged grain
5.8. Earhead bug, *Calocoris angustatus* (Leth.):	1 = No shrivelled grain 2 = 1-10% shrivelled grain 3 = 11-25% shrivelled grain 4 = 26-40% shrivelled grain 5 = More than 40% shrivelled grain
5.9. American bollworm, *Heliothis armigera* (Hubner):	Score 1-5
5.10. Corn earworm, *Heliothis zea* (Boddie):	Score 1-5
5.11. Other head feeders:	Score 1-5

Leaf feeders (insects):	1 = No leaf damage 2 = 1-10% plants with one or more leaves damaged 3 = 11-25% plants with one or more leaves damaged 4 = 26-40% plants with one or more leaves damaged 5 = More than 40% plants with one or more leaves damaged
5.12. Nutgrass army worm, *spodoptera exempta* (Walker):	Score 1-5
5.13. Fall army worm, *Spodoptera frugiperda* (J.E. Smith):	Score 1-5
5.14. Army worm, *Mythimna separata* (Walker):	Score 1-5
5.15. Greenbug, *Schizaphis graminum* (Rondani):	Score 1-5
5.16. Corn leaf aphid, *Rhopalosiphum maidis* (Fitch):	Score 1-5
5.17. Sugarcane aphid, *Aphis sacchari* (Zehnter):	Score 1-5
5.18. Chinch bug *Blissus leucopterus* (Say):	Score 1-5
5.19. White grubs *Phyllophaga crinita* (Burmeister) *Schizonycha* (spp.) *Holotrichia consanguinea* (Blanch)	Score 1-5
5.20. Webworms *Celama sorghiella* (Riley) *Stenachroia elongella*	Score 1-5

(Hamps.)
Eublemma (sp.)

Leaf feeders (mites):

1 = No damage
2 = 1-10% plants with one or more leaves damaged
3 = 11-25% plants with one or more leaves damaged
4 = 26-40% plants with one or more leaves damaged
5 = More than 40% plants with one or more leaves damaged

5.21.	*Oligonychus indicus* (Hirst):	Score 1-5
5.22.	*Oligonychus pratensis* Banks:	Score 1-5
5.23.	Other leaf-feeding mites:	Score 1-5

6. Disease Resistance Evaluation Data

6.1.	Charcoal rot, *Macrophomina phaseolina* (Tassi) Gold:	Score 1-5
6.2.	Downy mildew, *Peronosclerospora sorghi* (Kulk.) Weston and Uppal:	Score 1-5
6.3.	Leaf blight, *Exserohilum turcicum* (Pass.):	Score 1-5
6.4.	Anthracnose, *Colletotrichum graminicola* (Lesati) Wilson:	Score 1-5
6.4.1.	Foliage:	Score 1-5
6.4.2.	Head:	Score 1-5
6.5.	Rough leaf spot, *Ascochyta sorghina* (Saccardo):	Score 1-5
6.6.	Grey leaf spot, *Cercospora sorghi* (Ellis and Everhart):	Score 1-5
6.7.	Sooty stripe, *Ramulispora sorghi* (Ellis and Everhart) Olive and Lefebvre:	Score 1-5
6.8.	Rust, *Puccinia purpurea* (Cooke):	Score 1-5
6.9.	Zonate leaf spot, *Gloecercospora sorghi* (Barn and Edgerton):	Score 1-5
6.10.	Bacterial stripe, *Pseudomonas andropogoni* (E.F. Smith) Stapp:	Score 1-5
6.11.	Bacterial leaf spot, *Pseudomonas syringae* (Van Hall):	Score 1-5

6.12.	Sugarcane mosaic and maize dwarf mosaic:	Score 1-5
6.13.	Grain molds, *Fusarium* spp. *Curvularia* spp.:	Score 1-5
6.14.	Grain molds, *Phoma* spp.:	Score 1-5
6.15.	Ergot, *Sphacelia sorghi* (McRae):	Score 1-5
6.16.	Grain smut (covered: kernel smut), *Sphacelotheca sorghi* (Link) Clinton:	Score 1-5
6.17.	Long smut, *Tolyposporium ehrenbergii* (Kuhn) Patovillard:	Score 1-5
6.18.	Head smut, *Sphacelotheca reiliana* (Kuhn) Clinton:	Score 1-5
6.19.	Loose kernel smut, *Sphacelotheca cruenta* (Kuhn) Potter:	Score 1-5
6.20.	Other diseases:	Score 1-5

7. Others

7.1.	*Striga asiatica* (Linn.) Kuntze resistance:	1 = No damage 2 = 1-10% plants damaged 3 = 11-25% plants damaged 4 = 26-40% plants damaged 5 = More than 40% plants damaged
7.2.	*Striga hermonthica* (Benth.) resistance:	Score 1-5
7.3.	Reaction to drought:	Score 1-5
7.4.	Reaction to salinity:	Score 1-5
7.5.	Cold tolerance (seedling):	Score 1-5
7.6.	Cold tolerance (reproductive):	Score 1-5
7.7.	Nonsenescence: (green leaves at grain maturity)	1 = All leaves green 2 = Few lower leaves dead 3 = About half of leaves dead 4 = More than half of leaves dead 5 = All leaves dead
7.8.	Restoration response (Milo sources):	R = Restorer P = Partial restorer B = Nonrestorer
7.9.	Male-sterile (Cytoplasm systems):	1 = Milo 2 = Texas 3 = Maldandi

7.10. Low pH complex:	N = Resistant Y = Susceptible
7.11. Grain quality:	N = Normal W = Waxy S = Sugary P = High protein L = High lysine T = High tannin

GLOSSARY

A-line
cytoplasmic male-sterile seed parent used in making commercial hybrids.

accession
(a) cultivar registered at a genetic resources center;
(b) any entry newly received in a crop improvement program.

accessions collection
a collection in which seed of every entry is saved. This reduces the chance that genetic loss will occur through elimination of apparent "duplicates" and the masking of useful traits by bulking.

active ingredient (a.i.)
the active component of a formulated product such as a fungicide. For example, Ridomil 25 WP contains 25% of the active component acylalenine and 75% inert material. Thus Ridomil has 25% a.i.

additive genes
genes that do not show dominance over genes at other loci but have an accumulative effect.

additive variance
that component of genetic variance due to additive effects of the genes.

adventitious
arising from a position on a stem or at the crown of a cereal plant; often used in relation to roots.

aflatoxin
toxic metabolites produced by members of the *Aspergillus flavus—oryzae* group that are carcinogenic to various domestic and laboratory animals, including primates. Chemically, they are difuranocoumarin compounds.

allele
one of a pair or series of alternative expressions of a gene that may occur at a given locus on a chromosome.

alleyway
uncropped area that divides two or more blocks of cropped areas or plots in a field. Normally used as turning space for farm machinery and pathway for taking observations.

allopolyploid
polyploid having two separate genomes combined in the same nucleus.

alternate host
(a) either of two hosts of pathogens that must carry out different parts of their life cycles on different host species;
(b) one of two species of plants required as a host by a heteroecious rust fungus for completion of its development cycle.

alternative host
(a) one of several host species capable of being diseased by the same phase in the life cycle of one pathogen;
(b) plant other than the main host that is fed upon by a parasite; not required for the completion of the development cycle of a parasite.

anaphase
stage of cell division during which chromatids of chromosomes separate and move to opposite poles of the cell.

aneuploid
type of polyploidy in which one or more chromosomes are missing from, or duplicated in, the nucleus (e.g., 2n-2n, 2n+1, etc.).

anther
male part of the flower in which pollen is produced.

autopolyploid
a polyploid in which a single genome is replicated a number of times.

B-line
(a) fertile counterpart of the A-line. The B-line does not have fertility-restoring genes and is used as the male parent to maintain the A-line, i.e., A-line × B-line reproduces the A-line. The B-line is normally fertile and can be reproduced by self-pollination;
(b) maintainer of the A-line.

backcross
cross between a hybrid and one of its parents.

basic collection
working collection of lines very carefully chosen and stratified by race, subrace, geographical distribution, and ecological adaptation.

biological control
employment of enemies and diseases of a pest for purposes of maintaining adequate control. The artificial application of biotic control.

bivalent
pair of homologous chromosomes that have joined together during meiosis 1.

bulk
to grow and maintain genetically different plants in a population without separating them into pure lines or applying selection efforts.

bulks collection
assembly of similar material from a collection into one or more bulks. Special bulks might be created of entries with some special attribute, i.e., resistance or quality traits. Actually, entries in any one bulk should be similar in origin, height, maturity, and adaptation.

canopy
cover of leaves and branches formed by tops, or crowns, of plants.

canopy density
relative completeness of the canopy, usually expressed as a decimal coefficient, taking closed canopy as unity. The following classification of canopy density is in vogue: "closed" when the density is 1.0; "dense" when the density is between 0.75 and 1.0; "thin" when the density is between 0.5 and 0.75; and "open" when the density is less than 0.5.

centromere
that part of a chromosome to which the spindle is attached. Chromatids are joined at the centromere.

cereals
grain crops of the family *Gramineae* and food grains produced from them.

chiasma (pl. chiasmata)
point where chromatids in a bivalent join, and where substitution of segments occurs during crossing over.

chi-square
statistical test that can be used to determine whether an observed genotypic ratio is different from the ratio that would be expected if a given genetic system were operative.

chlorosis
unseasonable yellowing of foliage, symptomatic of a chlorophyll deficiency in leaf tissues under normal light conditions.

chromatid
one of the two identical units formed when a chromosome duplicates during meiosis or mitosis.

chromosomes
small structures in the nucleus of a cell that carry the genes. They appear as thread- or rod-shaped structures during metaphase. Each species has a characteristic number of chromosomes.

cleistogamy
pollination and fertilization in an unopened floret.

climatic analogs
areas alike with respect to some of the major weather characteristics affecting the production of crops.

climatic factors
radiation, light, air temperature, precipitation, evaporation, humidity, atmospheric pressure, and winds that affect the biosphere.

climax
plant community of the most advanced type capable of development under prevailing climatic and soil conditions.

clone
group of plants derived by asexual reproduction from a single parent plant. Such plants, therefore, have the same genetic constitution.

cluster bagging
at ICRISAT, a method of maintaining pearl millet germplasm by planting in clusters and bagging so as to facilitate intermating.

coefficient of variation or variability
statistical term, meaning standard deviation

expressed as a fraction of the mean or as a percentage.

collection
(a) collected sample;
(b) process of collecting germplasm.

collection, population
populations established as composite crosses in order to maximize recombination; these may or may not incorporate male-sterile lines. Such populations should not only conserve germplasm, but also evolve new base material for future work.

collection, working
sizeable collection of evaluated accessions that are adequately stored, documented, and available for immediate use.

collection, world
comprehensive collection of samples from different geographic areas of the world, held in storage for preservation (see accessions collection).

collector number
number assigned to an accession by the collector at the time of collecting.

colonization (pathology)
invasion of host tissues by a pathogen following the successful completion of infection.

combining ability
performance of an individual plant in a series of crosses (general combining ability) or the deviation from this in a specific cross (specific combining ability).

composite
genetic material developed by intermating (three to four generations) selected open-pollinated parent varieties or lines known for their diversity. Parents are selected on the basis of their per se performance of their general combining ability. Such constructed composite populations are made for use in recurrent selecting programs.

coniodiophore
specialized aerial hypha that produce conidia in certain ascomycetes and imperfect fungi.

conidium (pathology)
unicellular asexual reproductive fungal spore produced exogenously on a specialized hyphae (conidiophore).

continuous variation
variation that cannot be divided into separate classes.

conversion
changing tall photosensitive tropical germplasm into day-neutral shorter lines by a backcrossing program.

correlation coefficient
measure of linear correlation that can take values between +1 and −1: A value close to +1 indicates almost perfect positive association, high values of one variable occurring with high values of the other; a value close to −1 indicates almost perfect negative association; a value close to zero indicates absence of association.

coupling phase
a condition where linked dominant alleles are found on one homologous chromosome while their recessive alternatives are found on the other homologous chromosome.

cropping intensity (cropping index)
method of expressing the number of crops grown on the same piece of land; e.g., a monocrop is given a value of 100, a double crop a value of 200, and intercropping between rows in a full stand of a base crop, 150.

cropping pattern
yearly sequence and spatial arrangements of crops, including the alternation of crops and fallow, on a given area.

crop residue
that portion of a plant or crop left in the field after harvest, or that part of the crop that is not used domestically or sold commercially.

crop rotation
growing of different crops in recurring succession on the same land.

crossing over
process that occurs during meiosis 1 when segments of chromatids are exchanged between homologous chromosomes. It results in a recombination of the genes.

cultivar
a cultivated variety; a population within a cultivated plant species distinguishable from other

populations, produced by selection or hybridization (either primitive or advanced).

cytokinesis
division of the cytoplasm following the division of the nucleus in meiosis or mitosis.

cytoplasm
main contents of a cell in which the nucleus and other bodies are located.

damping-off
collapse and death of seedlings resulting from the development of a lesion on the stem or hypocotyl at soil level, or from the massive colonization of young seedling tissue.

deciduous
descriptive of plants or trees that shed leaves or awns at a particular season or stage of growth.

deficiency
absence of a segment of a chromosome.

defoliation
a reduction in the normal amount of foliage due to insect or fungal attack or other injury or spraying; may be partial or complete (applies to leaves only).

descriptor
standard term used in the genetic resources information language for a character.

descriptor state
refers to various states in which a descriptor can exist—for example, red, purple, white.

determinate growth
a growth pattern in which the plant first completes the vegetative phase of development and then enters the reproductive phase and all the seeds ripen approximately at the same time.

dihybrid
hybrid that is the result of crossing homozygous parents that differ with respect to two loci.

diploid
organism or cell with two sets of chromosomes.

discontinuous variation
variation that can be described by a number of separate classes, e.g., red or white, purple or green, etc.

documentation
process of recording facts and figures on germplasm collections on paper, punched card, or magnetic devices.

dominance
(a) situation in which one allele (the dominant allele) expresses itself to the exclusion of the contrasting (recessive) allele;
(b) dominant character: character that is expressed in a phenotype to the exclusion of the contrasting (recessive) character.

dominance variance
component of genetic variance that is due to dominance effect of genes.

double-cropping
growing a second crop in one growing season after the first crop has been harvested from the same piece of land (overlap between crops can occur; see "relay cropping").

drought (agricultural)
shortage of moisture for crop growth or animal production.

drought (general)
water shortage is basic to drought; it is a relative rather than an absolute condition.

drought (meteorological)
a rainless situation for an extended period during which some precipitation should normally have been received, depending upon location and season.

drought resistance
(a) a characteristic of plants suitable for cultivation in dry conditions, regardless of the inherent mechanism that provides resistance. One of the more important properties is the capacity to endure, without injury, an intense loss of water;
(b) relative ability to maintain growth and yield under moisture-stress conditions.

dryland farming
the practice of crop production in low-rainfall areas by conserving natural precipitation. Supplemental irrigation may be given from harvested runoff water.

duplication
presence of a segment of a chromosome more than once on the same chromosome.

E.C. Number
Exotic Collection Number assigned by Plant Introduction Bureau, Government of India.

ecology
the study of interrelationships of organisms to one another and to the environment.

economic protection
protection of crops from pest damage only to the extent that the resultant economic gains exceed the costs of protection.

ecosystem
community of plants and animals, including humans, within a habitat, and their relations to one another.

ecotype
local race (ecological race) with genotypes adapted to a particular restricted habitat as a result of natural selection within the local environment.

egg
female gamete.

embryo
the part of a seed from which the root and shoot system of the plant come after germination.

endemic
refers to a disease that is permanently established in moderate to severe form in a defined area (commonly a country or part of a country).

endosperm
nutritive tissue arising in the embryo sac after the fusion of a haploid nucleus from the pollen with a diploid nucleus in the embryo sac.

environment
sum total of all external conditions that may act upon an organism or community to influence its development or existence.

ephemeral
short-lived annual capable of achieving maturity within a few weeks after germination. Ephemerals are able to avoid drought stress by completing their life cycle within a brief rainy period.

epidemic
widespread temporary increase in the incidence of an infectious disease.

epidemiology
study of factors affecting outbreak and spread of infectious diseases.

epistasis
(a) suppression of genes at one locus by a dominant gene at another locus;
(b) any nonallelic gene interaction.

euploid
polyploid with an exact multiple of the basic (n) number of chromosomes.

evaluation
process of determing potential of a collection or accession.

evaluation descriptors
characters utilized to evaluate an accession; may include morphological as well as agronomic characters.

exotic
not native to a given area.

experimental variety
analog of a synthetic. Variety produced by intermating a few (fewer than ten, often four or five) selected composite progeny. (Composite progeny are not inbred lines, as are normally used for synthetics.)

F_1
generation that arises from a given crossing; the filial generation.

F_2
generation produced by selfing the F_1; the second filial generation.

factor
term used in Mendelian genetics, equivalent to the allele.

fertilization
fusion of a male with a female gamete to form a zygote.

flag leaf
last fully expanded leaf in a cereal plant. Prior to emergence of the head, the flag leaf surrounds the head and is then called a boot leaf.

fodder crop
crop grown for feeding to animals.

forage
in range management, unharvested plant material of any kind available for animal consumption. It may be used for grazing or be cut for feeding. When cut, it becomes feed (hay or silage).

frequency (statistics)
number of observations assigned to any of an arbitrary set of classes.

full-sib
term used in population improvement. A full-sib family comprises progeny from a cross between two selected plants within the population. In sorghum improvement, the cross is frequently made between a male-fertile and a male-sterile plant.

gain
a measure, usually expressed as a percent, giving the difference in the expression of a trait under selection from one generation to the next.

gamete
mature male or female reproductive cell. The male gamete is the pollen grain and the female gamete is the egg.

gametogenesis
formation of the gametes.

gene
unit of inheritance, located on a chromosome. Genes control the expression of characters, either individually or in combinations.

gene park or nature reserve
isolated protected area used to conserve the genetic resources of wild relatives and weedy companions of a crop species in a natural state.

gene pool
useful genes or gene complexes in a divergent population.

generation
one complete life cycle. The generation begins with the formation of the zygote and ends when the resulting plant dies.

genetic resources
sum total of the genetic material in a species.

genetics
science of heredity and variation.

genetic stock
variety or strain known to carry one or more specific traits.

genetic stock collection
stocks with known genes, translocations, inversions, additions, or substitutions, and lines with resistance or tolerance to known races of pathogens, insects, or weed pests.

genome
complete set of (n) chromosomes, which are inherited as a set from parents in diploid species.

genotype
genetic constitution of a plant.

germination
resumption of growth of seed or spore. Usually recognized by rupture of the seed coat or spore wall and appearance of a radicle, hypocotyl, or thallus.

germination percentage
general term for the percentage of seeds within a sample that actually germinate.

germplasm
entire array of cultivars in a crop species, related wild species in the genus, and hybrids between the wild and cultivated species.

germplasm conservation
collection and preservation (in a long-term repository) of world genetic resources.

grain
seed of agricultural crops (in bulk) harvested and used domestically or commercially.

growing season
period(s) of the year during which crops grow and mature.

habitat
(a) sum of effective environmental conditions

under which an organism lives;
(b) often used for natural range or distribution of species;
(c) kind of place in which a plant or animal lives—such as forest habitat, grassland habitat, etc.

half-sib
term used in population improvement. A half-sib family comprises progeny from a cross of bulk pollen onto a selected parent—that is, only one parent in the cross is identified (selected). In sorghum improvement work, bulk pollen frequently comes from a pool of selected entries either by open pollination in isolation or by hand crossing bulk pollen onto genetic male-sterile plants (the selected parents).

haploid
cell or an organism having only one genome (n chromosomes).

harvest index
ratio of dry matter in the grain to total above-ground dry matter.

hectare
standard area measure in the metric system, 10000 square meters in area.

heredity
transmission of characters from parents to offspring.

heritability
measure of the degree to which a character is controlled by the genotype as compared to the environment.

heteroecious
requiring more than one host for a complete development cycle (e.g., rust fungi).

heterosis
extra vigor that is often expressed in hybrids.

hexaploid
euploid plant that has six genomes, i.e., six sets of chromosomes (6n).

homologous chromosomes
chromosomes that have the same structure and the same loci and that pair during meiosis. In a diploid, one homologous chromosome of each pair is derived from the male parent and the other from the female.

homozygous
having identical alleles at corresponding loci on homologous chromosomes.

hybrid
plant resulting from a cross between parents that are genetically unalike.

hybridization
crossing of one plant with another. Crossing between plants of the same species is called intraspecific hybridization and crossing between different species is called interspecific hybridization.

hybrid vigor
increased vigor of growth in a cross between two genetically different parents, as compared with growth in either of the parents.

hypersensitivity
violent reaction of an organism to attack by a pathogenic organism or a virus, resulting in prompt death of the invaded tissues, thus preventing further spread of the infection. Hypersensitivity is the extreme case of susceptibility and as such is the opposite of immunity, although the two terms are often mistakenly used as synonyms.

hyperparasite
organism that parasitizes another parasite.

IBPGR
International Board for Plant Genetic Resources.

immune
exempt from infection, protected against a disease by an innate or acquired immunity.

immunity
total exclusion of the potential pathogen so that the potential host is completely free from disease. A plant that is infected but not showing symptoms may be resistant but is not immune.

inbreeding
selfing or crossing between closely related plants for one or more generations.

incipient wilting
small loss in turgidity during warm weather, even when soil is moist. May not be visible to the naked eye. Usually reversible at night.

infect
to enter and establish a permament or temporary parasitic relationship with an organism.

infection
at the epidemiological level of the pathosystem, infection refers to the contact made between host and parasite; hence, auto-infection, allo-infection. At the histological level, infection refers to the process of penetration of a host by a pathogen.

infest
to overrun the surface of a plant, or to be dispersed through soil or other substrate.

inoculation
the introduction of living or killed organisms, usually microorganisms, into a new environment such as soils, culture media, or the living body of a higher organism, animal or plant.

inoculum
material containing microorganisms or virus particles to be introduced into or transferred onto a host or medium. Term also refers to potentially infective material available in soil, air, or water and that can result in natural inoculation of the host.

intensive protection
protection of crops from pest damage to the extent that such damage is negligible and does not impede precise measurement of research parameters.

inter-
between things of a different kind; e.g., interspecific = between different species, interallelic = between different alleles.

intermediate inheritance
inheritance in which the heterozygous plant differs from either of the homozygous parents.

interphase
resting stage of a cell between meiotic or mitotic divisions; stage following telophase prior to next prophase.

intra-
within things of the same kind; e.g., intraspecific = within the same species.

introgression
incorporation of genes of one species into the gene pool of another species by hybridization and backcrossing.

invasion
the penetration and colonization of a host by an organism.

inversion
rearrangement of a segment of a chromosome so that it is the opposite way around.

IP number
international pearl millet number. Every accession in the pearl millet germplasm collection is identified by an IP number.

IS/GR
Information Systems/Genetic Resources program, University of Colorado, Boulder, Colorado, USA.

IS number
international sorghum number. Every accession in the world sorghum germplasm collection is identified by an IS number.

isolate
(a) to separate a microorganism from host or substratum and establish it in pure culture;
(b) a single pure culture of a microorganism.

line
group of individuals from a common ancestry.

linkage
association of two or more genes that are located on the same chromosome and tend to be inherited together.

locus (loci)
fixed position on a chromosome that is the location of a particular gene or one of its alleles.

M_1
the generation following a mutation.

maintenance
continuity of an accession in its original form through careful growing out and proper storage.

male sterile
describes the complete or partial failure of a male

plant to produce mature reproductive pollen cells.

map unit
crossing over of 1% is sometimes referred to as one map unit.

marker gene
gene of known function and known location on the chromosome.

mass selection
term used in population improvement: individual plants in the population are selected; seeds of the selected plants are bulked to form a population for the next cycle; the process repeats.

maternal
relating to the mother.

mean, arithmetic
the result of adding together a set of values and dividing by the number of values, due regard being paid to the sign.

median
value of a variate such that equal numbers of observations are less than and greater than the value.

meiosis
process of cell division where the daughter cells have half the number of chromosomes of the parent cell. It is also called reduction division.

metaphase
stage of cell division when the chromosomes come to lie on a plane through the center of the cell.

minimum descriptors
standard set of descriptors established on a global basis for evaluating germplasm of a particular crop.

mitosis
process of cell division in which the daughter cells have the same number of chromosomes as the parent cells.

modifying gene
gene that affects the expression of another gene.

monohybrid
An F_1 that is heterozygous at one locus.

monoploid
plant with only the diploid number of chromosomes (n).

monosomic
plant that lacks one chromosome (2n-1).

multiple alleles
three or more alternative alleles that can be present at a given locus.

mutable genes
genes with a very high mutation rate.

mutagen
physical or chemical agent that increases the mutation rate.

mutant
cell or plant which is the result of a mutation.

mutation
heritable change in the genetic material, either a change in the chromosomes or in the genes.

n: number of chromosomes that make up one genome. It is called the basic, haploid, or monoploid number.

nick
the simultaneous flowering of both parents in a cross.

nucleus
body in a cell that contains the chromosomes.

nullisomic
(a) having one homologous pair of chromosomes (2n-2);
(b) a nullisomic individual.

octoploid
plant with eight genomes in the nucleus (8n).

off type
refers to plants that differ in morpho-agronomic characters from the majority or representative plants of a variety, for instance admixtures in a field and obvious contaminants such as tall plants in the semi-dwarf cultivar or vice versa.

ontogeny
course of development of an individual organism (the ontogenetic phase of agricultural crops

relates to the seed formation and seed-setting phase).

out-breeding
crossing between two plants with different genotypes.

ovule
structure in a flower that contains the female gamete (egg) and that develops to form the seed after fertilization.

P: symbol used to indicate a parent.

panicle
in a cereal crop, that portion of the plant that bears seeds.

parasite
organism that lives in or on and derives nutrients and/or shelter from an organism of a different species.

passport descriptors
characters assigned to an accession in the process of collection.

paternal
relating to the father.

pedigree
nomenclature assigned to breeders' material.

pedigree breeding
(a) system of breeding in which individual plants are selected in the segregating generations from a cross on the basis of their desirability, judged individually and on the basis of a pedigree record;
(b) a process of head rowing; i.e., seeds from a selected head in one season are sown in a row during the same season of the next year.

pest
any organism of animal or plant origin known or suspected or likely to be harmful to plants. Includes any insect, nematode, snail, bacterium, fungus, virus/mycoplasma, phanerogam, and weed.

phenology
study of time of appearance of characteristic periodic events in the life cycles of organisms in nature and of how these events are influenced by environmental factors.

phenotype
observable or measurable characters of an organism.

pheromone
substance secreted by an insect that influences the behavior of other individuals of the same species.

photoperiodism
response in the ontogeny of an organism to the relative duration of day and night. Many plants have specific requirements of relative length of daily light and dark periods for floral initiation and seed set.

pleiotropic gene
a gene that affects more than one character.

point mutation
mutation of a single gene.

pollen
male gamete of a plant that is produced in the anthers.

pollination
transfer of pollen from the anther to the stigma. Pollination must occur before fertilization can take place.

pollinator
line or population used as a male parent (pollen donor).

polygenes
(a) a relatively large number of genes that occur at different loci but that affect the same character so that distinct classes in an F_2 population are not identifiable;
(b) genes involved in quantitative inheritance.

polyploid
plant having more than the diploid (2n) number of chromosomes.

population
(a) group of individuals (plants) within a species or a variety that are found at one site or field. Plants in the population may or may not be genetically alike;
(b) group of intermating individuals that share a common gene pool;
(c) community of random-mating individuals

that share a common gene pool. Populations can be either natural (as landrace varieties) or artificial (as composites or synthetics) in origin.

probability
chance of an event occurring.

progeny
literally, the offspring of a single plant. This plant may have been either selfed or crossed in various ways. In recurrent selection, progeny may be half-sibs, full-sibs, reciprocal full-sibs.

progeny testing
(a) term used in recurrent selection. A number of progenies representing a population are produced (by selfing, sib-mating, crossing to a tester—depending upon the objective) and evaluated in one or more environments to determine which are the best progeny to recombine to produce an improved population;
(b) method of assessing the genetic character of an individual by the performance of its progeny.

prophase
first stage of mitosis and meiosis during which the chromosomes appear.

protogyny
(a) maturation of pistils before anthers;
(b) where female parts of flowers are receptive before the male parts of the flowers on the same plant produce pollen (a system favoring cross-pollination).

pure line
group of plants that have nearly the same homozygous genotype, and that breed true.

quadrivalent
where four chromosomes instead of the normal two (bivalent) join together during meiosis.

quantitative character
a character that shows continuous variation and that cannot be classified into separate classes.

quantitative inheritance
inheritance of quantitative characters.

R-line
this line, when crossed to the A-line, produces a male-fertile F_1 hybrid. This is the hybrid sown by the farmer.

rabi season
the season (postmonsoon) in which crops are grown mostly on moisture stored in the soil, with or without significant winter rainfall. Commences with the termination of the rainy season, usually in October. At ICRISAT, the appropriate term is "postrainy" season (see "growing season").

random mating
situation in which every plant in a population has an equal chance of mating with any other plant in the population.

ratoon crop
crop obtained from regrowth from stubble (living stumps) following a harvest, not necessarily of grain. Examples include sugarcane, sorghum, rice, millet, oats, and pigeonpea.

ratooning
cutting a plant to obtain regrowth.

recessive (breeding)
(See "recessive allele.")

recessive allele
(a) an allele not expressed in the heterozygous state when a dominant allele is present at the same locus on the other homologous chromosome;
(b) an allele masked by the effect of another—specifically, an allele the effects of which are masked by a dominant allele.

reciprocal full-sib
full-sib made between selected plants from different populations; i.e., a cross is made A × B and B × A.

reciprocal recurrent selection
where recurrent selection is between two genetically different populations with an objective of improving the populations simultaneously for both general as well as specific combining ability. This is mainly to increase the population cross performance or the performance of hybrids made between inbreds developed from the two populations.

recombination
a combination of characters in an offspring different from that of either parent.

recurrent selection
(See "selection, recurrent.")

reduction division
(See meiosis.)

relay cropping
seeding of a second crop between the rows of a standing crop shortly to be harvested.

repulsion phase
in linkage, where a dominant allele is linked to a recessive allele in each homologue.

resistance
ability of an organism to withstand or oppose the operation of or to reduce or overcome the effects of an injurious or pathogenic factor. For plant pathogens, resistance can be defined as the ability of the host to suppress or retard the activity of a pathogenic organism or virus. Resistance is a quantitative phenomenon and is the inverse of susceptibility. Thus resistance can vary from high (low susceptibility) to low (high susceptibility). Moderately resistant is equivalent to moderately susceptible. The term "tolerance" should not be used to define these intermediate reactions.

S_1
term used in population improvement. Symbol for designating the first selfed generation from an ancestral plant, S_0. The S_1 family comprises progeny from a selected male-fertile plant, the male-fertile plant being progeny from a half-sib. The S_1 is equivalent to an F_2. In sorghum, open-pollinated male-fertile plants in the population are used to establish S_1 families. Seeds for S_1 progenies are obtained by selfing selected plants in the half-sib progenies or random-mated bulk.

S_2
term used in population improvement. Symbol for designating the second selfed generation from an ancestral plant, S_0. The S_2 family comprises progeny from a selected S_1 plant. The S_2 is equivalent to an F_3. Seeds for S_2 progenies are obtained by selfing individual selected plants from S_1 progenies.

savannah
tropical or subtropical grassland with scattered trees, either as individuals or in clumps. Often a transitional phase between true grassland and forest.

screening
(a) separation of the unusable from the desirable;
(b) search for desirable characters or properties—for example, in relation to varieties and cropping systems.

seed
grain that has been selected, cleaned, and often treated for planting to grow a commercial crop.

seedling vigor
seedling growth rate.

segregation
separation of maternal and paternal chromosomes at meiosis to form the gametes, and the union of the gametes to produce new combinations at fertilization.

selection differential
(a) difference between the mean of the selected sample and that of the population from which it was selected;
(b) in recurrent selection, the mean phenotypic value of the progenies selected as parents (for recombination) expressed as a deviation from the population mean; that is, from the mean phenotypic value of all the progenies in the parental generation before selection was made. Expressed as percentage over population mean.

selection, mass
term used in population improvement:
(a) individual plants in the population are selected; seeds from the selected plants are bulked to form the population for the next cycle. The process is repetitive;
(b) form of selection in which individual plants are chosen on the basis of their phenotype and the next generation propagated from the aggregate of their seeds. The process repeats.

selection, recurrent
term commonly used in population improvement. It is a method of breeding designed to concentrate favorable genes scattered among a number of individuals by selecting in each generation among the progeny produced by matings inter se of the selected individuals (or their selfed or sibbed progeny) of the preceding generation. When this breeding method involves progeny

testing (mass selection does not), then each cycle has three steps—
(1) production of progenies by selfing or using any system of mating;
(2) evaluation of progenies; and
(3) recombination of the selected progenies. Selection continues cycle after cycle, provided sufficient variability remains.

self-fertilization
fertilization of an egg by a pollen grain from the same plant (see "selfing").

selfing
plant breeding term usually meaning natural or artificial self-pollination.

self-pollination
transfer of pollen from the anther to the stigma of the same flower or of another flower on the same plant.

semi-arid tropics
seasonally dry tropical areas where monthly rainfall exceeds potential evapotranspiration for 2 to 7 months and the mean monthly temperature is above 18°C. The areas with 2 to 4½ wet months are called dry semi-arid tropics, and those with 4½ to 7 wet months are called wet-dry semi-arid tropics.

sibbing
sib-mating. Cross between plants from the same population. Generally pollen is collected from several plants from the same population, bulked, and crossed onto sister plants of the same population.

sibling
one of two or more offspring of the same parents.

sib-mating
crossing siblings, two or more individuals of the same parentage (brother-sister mating).

sidecar
a special-purpose breeding population containing a particularly desirable character (such as resistance to a specific disease); the sidecar population is improved agronomically and then introduced into, or becomes, the main breeding population.

significance test (statistics)
a calculation of the probability that an ascertained quantitative difference between the results of certain experimental treatments is of a magnitude to justify attributing it to the difference in treatment rather than to chance or to experimental error. If this probability is less than an agreed small value (termed "level of significance" and often accepted as 1 in 20), the difference is said to be significant. (Note: a nonsignificant difference does not imply a proof that a difference between treatments does not exist.)

somatic cells
normal plant cells that are generally diploid and not including the cells that give rise to gametes.

standard deviation
measure of the average variation of a series of observations of a population about their mean. In normally distributed sets of moderate size, the interval of the mean, plus or minus the standard deviation, includes about two-thirds of the observations.

susceptibility
inverse of resistance. Defined as the inability of the host to defend itself against or to overcome the effects of invasion by a pathogen or virus. If a cultivar is seen with no symptoms and it is not known that the cultivar has been challenged by a particular pathogen, it cannot be said that the cultivar is resistant; the proper description is "free of symptoms."

symbiosis
the living together in more or less intimate association of two dissimilar organisms, with a resulting mutual benefit. Common examples lichens (algae and fungi) and leguminous plants living in association with rhizobia.

synthetic
(a) advanced generation random-mating population derived from a few selected inbred lines;
(b) a variety produced by crossing inter se a number of inbred lines (usually five to eight) selected for their good general combining ability. The variety is subsequently maintained by open pollination.

telophase
last stage of meiosis or mitosis: the chromosomes are at the poles of the cell, and a nuclear membrane forms around them.

testcross
cross made with a homozygous recessive parent to determine whether an individual is homozygous or heterozygous.

tetraploid
polyploid plant having four genomes (4n).

tiller
erect or semierect branch arising from a bud in the axils of leaves or at the base of a plant.

tolerant
term used to describe the ability of the host plant to withstand unrestricted and extensive colonization by a parasitic organism or virus without symptom development. "Tolerant" is not to be used to describe moderate susceptibility or moderate resistance in a plant.

topcross/tester
cross between a selection, line, clone, etc., and a common parent, which may be called a variety, inbred line, single cross, etc. The common parent is called the tester parent.

transgressive segregation
appearance of plants in the F_2 or later generations having a character outside the range of the parents.

translocation
interchange of a small segment of a chromosome with a segment from a nonhomologous chromosome.

trisomic
describes a diploid plant having an extra chromosome (2n+1).

trivalent
unit of three homologous chromosomes that may be formed during pairing in meiosis in polyploids.

univalent
describes a chromosome that remains unpaired during meiosis.

variance
statistical measure of variation. Equal to the square of the standard deviation.

variation
occurrence of differences between individuals of the same species.

variety
(a) population of plants having many characteristics in common; a variety may be a pure line, a mixture of pure lines, a Mendelian population, or a clone;
(b) a group of plants within a species that differ in certain characters from other groups in the same species, i.e., plants that have some character (usually desirable) in common. (The International Code of Botanical Nomenclature now distinguishes between a botanical variety that has not undergone human manipulation and a cultivated variety [See *cultivar*] that has originated and persisted under cultivation.)

weed
a plant out of place. Any plant growing where not wanted.

weedy types
unwanted types accompanying the cultivated crop that have a spontaneous spreading habit and interact with the cultivated race as well as with the truly wild races.

wild types
naturally occurring nondomesticated crop relatives.

working collection
(See "collection, working.")

xenia
immediate effect of pollen on the endosperm.

xerophyte
a plant that can subsist in dry situations.

yield components
primary yield determinants: panicle number, grain number of panicle, and individual grain weight.

yield (crop)
useable portion(s) of a crop; has value for on-farm use or for marketing.

zygote
cell formed by fusion of the male and female gametes at fertilization.

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