GENETICS OF GRAIN-MOULD RESISTANCE AND YIELD COMPONENTS IN SORGHUM (*Sorghum bicolor*) VARIETIES

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DEDICATED TO MY PARENTS

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CERTIFICATE

THIS IS TO CERTIFY THAT the Thesis entitled **"Genetics of Grain-mould Resistance and Yield Components in Sorghum (*Sorghum bicolor*) Varieties"**, submitted for the degree of Doctor of Philosophy in Genetics of Osmania University, is a record of the bonafide research carried out by **Mrs. S Audilakshmi** under my supervision, and no part of thesis was submitted for any other degree or diploma.

The assistance and help rendered during the course of this investigation and the source of literature have been fully acknowledged.

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DECLARATION

I hereby declare that the research work presented in this thesis, entitled **"Genetics of Grain-mould Resistance and Yield Components in Sorghum (*Sorghum bicolor*) Varieties"**, has been carried out by me in the Department of Genetics, Osmania University, Hyderabad - 500007, under the supervision of Prof. T. Papi Reddy. The work is original and no part of the thesis has been submitted earlier for any other degree or diploma of any university.

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(S. Audilakshmi)

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Introduction

1 INTRODUCTION

Sorghum (*Sorghum bicolor* (L.) Moench) is grown worldwide for food, feed, fodder, fuel and industrial products. It is cultivated widely throughout tropical, subtropical and temperate regions between latitudes 45° N and 45° S. Roughly 95 percent of the world's sorghum area lies in developing countries, mainly in Africa and Asia (ICRISAT and FAO, 1996). This crop is primarily grown in agroecologies subject to low rainfall and drought, predominantly by subsistence farmers.

In India, sorghum is the most important cereal for poor people in semi-arid zones. It is grown in the states of Maharashtra, Karnataka, Andhra Pradesh, Tamil Nadu, Gujarat, Madhya Pradesh and Uttar Pradesh. Widespread adoption of high yielding hybrids in Maharashtra, Karnataka, Tamil Nadu, Madhya Pradesh and Uttar Pradesh increased the yield levels by 2 to 3 fold.

The genus *Sorghum* is characterized by a vast and diverse germplasm pool; the immense morphological diversity of the cultivated races has emerged because ofvariable climate and geographical exposures in which its wild ancestors evolved,coupled with selection pressures imposed by the environment and by man fordomestication (Duncan *et al.*, 1991). Domesticated sorghum has resulted through direct selection from principally one or two wild races in Africa (de Wet *et al.*, 1970). Snowden (1936) and Harlan and de Wet (1972) postulated that sorghum emerged

from separate centers of origin and they subdivided the cultivated sorghums into morphologically distinct races: bicolor, guinea, caudatum, kafir and durra. They speculated that the race durra and bicolor arose from the wild subspecies *aethiopicum*, the kafirs arose from *verticilliflorum*, and the guineas evolved from *arundinaceum*.

Since there is immense morphological diversity of the cultivated sorghum, due to natural introgression, geographical isolation and disruptive selection, utilization of wild species is limited. In USA, among lines or hybrids released for commercial production, 21% had unadapted cultivar parentage and less than 1% had wild parentage (Duncan et al., 1991). Wild species have been utilized for green bug resistance (Bramel-Cox *et al.*, 1986) and for shoot fly resistance (Nwanze *et al.*, 1990).

Sorghums in the tropics have evolved in a hostile environment where unreliable rainfall, poor soils, pests, diseases and parasitic weeds all constantly exert harsh selection pressures. The traditional cultivars may not be high yielding under optimum conditions but they have a high survival value in unfavourable conditions. These cultivars are photosensitive long-duration types and are generally high biomass producers with poor grain yields. Therefore, the production of relatively short-duration photoperiod-insensitive sorghums has become the primary objective of almost all sorghum improvement programmes. The major genotypic changes

brought about during the 1960s triggered cultivar-input-management interaction and resulted in quantum jumps in productivity; they also imparted stability to production and enabled adoption of new cropping systems leading to more efficient land and water use (Rao, 1982). In India, sorghum hybrids were developed from temperate × tropical crosses by manipulating height and maturity genes and the critical stages of growth, *viz,* seedling, flowering and grain filling, coinciding with periods of assured rainfall. This resulted in quantum jump in productivity from 560 kg/ha in 1970 to 1020 kg/ha in 1996. The changes in area, production and productivity of *kharif* sorghum in India over 25 years are presented in Table 1. Though the productivity increased, the area under cultivation decreased from 1,15,22,000 ha in 1970 to 61,88,000 ha in 1996.

Table 1. Area, production and productivity of *kharif* sorghum in India.

	TE 1970	1992-93	1993-94	1994-95	1995-96	TE 1996
A	11522	7498	6838	5949	5778	6188
P	6456	9178	7284	5874	5860	6339
Y	560	1224	1065	988	1014	1022

Reproduced from the AICSIP Progress Report 1997. A = area (000 ha); P = production (000 t); Y = yield (kg/ha); TE = triennium ending.

Plate 1

The decrease in area of cultivation is due to low demand for food, limited commercialization, limited yield increases and grain mould susceptibility (Rana *et al.*, 1997). In AICSIP trials in 1986, the check and top ranked hybrid, CSH 9, yielded 3413 kg/ha (AICSIP). In 1996, the top ranked hybrid, MLSH 14, produced 3945 kg/ha (AICSIP), showing only 14% yield increase in 10 years. Incidentally, both hybrids are highly susceptible to grain moulds. Hence there is a need for developing high yielding grain mould resistant hybrids so as to break the yield plateau. Also such resistant hybrids should have good grain quality to meet the needs of domestic as well as international markets. Since there is a low utilization of *kharif* grain for food, the grain can be exported to other countries. As the standards for importation by other countries are very stringent, the strengthening of genetic resistance to grain moulds may be useful to promote export (Rana *et al.*, 1997).

Sorghum grain mould disease is caused by a complex range of fungi including *Fusarium moniliforme* (Sheld.), *Curvularia lunata* (Wakker) Boedijn, and *Phoma sorghina* (Sacc.) Boerma *et al.* (Castor and Frederiksen, 1980; Forbes *et al.*, 1992). The most obvious symptom of grain mould is the appearance of pink, orange, grey, white or black discoloration on the grain surface, depending on the specific fungal species present (Plate 1).

Losses due to grain mould are both quantitative and qualitative (Esele, 1995). Quantitatively, grain mould causes substantial yield losses. Annual global losses to

grain mould have been estimated as US $ 130 million (ICRISAT, 1992), and in India losses in grain yield have been estimated to be 30% (Murty and Rana, 1993). Qualitatively, grain moulds result in mouldy and discoloured pericarp leading to low price of the produce, a soft and chalky endosperm, sprouting (reduced germination of seed), decreased grain filling and size, mycotoxin, decreased test weight besides altered chemical composition (Glueck and Rooney, 1980; Williams and Rao, 1981; Jambunathan *et al.*, 1986). Hence breeding grain mould resistant hybrids may help to break yield stagnation, create good profitability, better recovery of industrial products and promote the export of good quality of grain.

Knowledge of resistant sources, mechanisms of resistance, characters associated with resistance, number of genes involved in resistance and the type of gene action, help in deciding the breeding procedure to be followed to incorporate resistance into high yielding background.

In view of the above, the present investigation has been undertaken with the following objectives.

1. To screen sorghum genotypes for grain mould resistance.
2. To evaluate sorghum genotypes for morphological and biochemical characters associated with grain mould resistance.

3. To study correlations between grain mould resistance, and morphological and biochemical characters.
4. To determine the genetics and inheritance pattern of grain mould resistance genes by generation mean analysis.
5. To analyze the genetics of characters associated with resistance by generation mean analysis.
6. To determine the genetic basis of grain yield and yield components in two susceptible × resistant crosses.

Review of Literature

2 REVIEW OF LITERATURE

Grain mould in sorghum is caused by a complex of fungi. From observations and studies in the USA, Africa and India, it is evident that *Fusarium moniliforme, Fusarium semitectum* and *Curvularia lunata* are the major causal agents of sorghum grain moulds (Murty *et al.,* 1980; Williams and Rao, 1981; Anonymous, 1976).

Castor and Frederiksen (1980) reported that in Texas the predominant field fungi in decreasing order of prevalence belong to the genera *Alternaria, Fusarium, and Curvularia.* It is thought that only a few fungi infect sorghum spikelet tissues during the early stages of grain development. These are, in approximate order of importance, *Fusarium moniliforme* (Sheld.), *Curvularia lunata* (Wakker) Boedijn, *F. semitectum* Berk., and Rav., and *Phoma sorghina* (Sacc.) Boerma *et al.* (Forbes *et al.,* 1992).

Symptoms: Colonization occurs primarily on the exposed part of the grain. Post-maturity colonization is generally what produces the "mouldy appearance" of grain maturing in humid environments (Forbes *et al.*, 1992). Fungal colonization of sorghum grain by different fungi produce a different set of symptoms. The colour of the mouldiness depends on the fungi involved. *F. moniliforme* produces pinkish-white to orange-powdery fungal growth on dry infected sorghum seeds. *Phoma sorghina* produces black pycnidia scattered over the surface of infected seed.

Curvularia lunata appears as a shiny, velvety black, fluffy growth on the grain surface (Bandyopadhyay, 1986).

Losses: Losses caused by grain mould are both quantitative and qualitative (Esele, 1995). At ICRISAT Asia Center, Patancheru (India), losses of up to 100% in highly susceptible cultivars have been experienced (Williams and Rao, 1981). In Texas (USA), unusually heavy rains at grain maturity during 1976 affected 400,000 ha of sorghum, and caused a loss of $46 million (Castor and Frederiksen, 1980). In another report, annual global losses to grain moulds have been estimated at US$130 million (ICRISAT, 1992). Sundaram *et al.* (1972) stated in their report on a survey of sorghum and millet diseases in India, in hybrid sorghums, losses of up to 50% due to head moulds were observed in experimental plots at Coimbatore (India). Denis and Girard (1980) reported results of comparison of yield and mould infection at three sites in Senegal. They found that when there were few other limiting factors to plant development, grain moulds had a clear negative effect on yield. Glueck and Rooney (1976) and Glueck (1978) reported variability in 1000-grain weight from 19.3 g to 33.5 g and of test weight from 47.3 to 62.2 lb bu^{-1} under severe weathering conditions of Texas A&M. Singh and Agarwal (1989) reported that 100-seed weight was reduced to 67, 43 and 40% by *C. lunata, F. moniliforme* and *P. sorghi* respectively. Preharvest sprouting may also occur under prolonged rainfall, high humidity and alternate wetting and drying conditions (Castor and Frederiksen, 1980; Forbes *et al.*, 1992). This leads to loss of seed viability and enhances the

development of grain moulds, thus causing chalkiness of the grain and loss of weight (Castor and Frederiksen, 1977; Maiti *et al.,* 1985). Qualitatively, grain mould results in a loss of grain market value (Anonymous, 1976; Castor and Frederiksen, 1980; Forbes *et al.,* 1992). In villages in Central India the market prices of sorghum grain were significantly related to degree of mould infection, and the prices of the mouldy grain was about 20% less than that of the cleanest grain (von Oppen and Jambunathan, 1978). The mouldiest of the grain in these samples was, however, not nearly as severely moulded as grain from many improved sorghum cultivars in our grain mould screening nurseries. Williams and Rao (1981) recorded, in addition to actual weight loss caused by grain mould infection, losses in marketable yield occur due to reduction in consumer acceptability, even with moderately moulded grain.

Sorghum grain deterioration from mould infection results in physiological and chemical changes (Glueck *et al.*, 1977). The fungi also cause reduction in seed viability, reduction in kernel size, kernel density, and increase in electrolyte leachate (Murty *et al.,* 1980; Castor and Frederiksen, 1981; Ibrahim *et al.,* 1985; Maiti *et al.,* 1985; Singh and Makne, 1985; Singh and Agarwal, 1989; Forbes *et al.,* 1992).

Loss in viability of moulded sorghum grain and reduction in seedling vigour are reported by many workers (Arif and Ahmed, 1969; Narasimhan and Rangaswamy, 1969; Tripathi, 1974; Mathur *et al., 1*975; Castor, 1977; Rao and Williams, 1977).

Fungus-infected seed often exhibit reduction in germination and emergence which cause poor stands in farmers' fields (Bhatnagar, 1971; Castor, 1977). In addition, seedlings may be killed after emergence, or their growth may be reduced (Bhatnagar, 1971).

Fungi such as *F. moniliforme* and *C. lunata* secrete enzymes that can degrade endosperm (starch) and germ tissues; the process is often accompanied by visibly moulded kernels (Wadje and Deshpande, 1976). In moulded grain, soluble carbohydrates are usually decreased as they are utilised to provide energy for growth and development of fungi (Glueck and Rooney, 1976). Somani *et al.* (1993) reported that crude protein was slightly reduced but crude fat, starch and ash contents were significantly reduced in moulded seeds. Moulds also alter the composition of phenolic compounds (Waniska *et al.*, 1992).

Grain moulds produce chemicals that are toxic to man and animals. The species of *Fusarium* produce zearalenone, a mycotoxin which has oestrogenic properties and which has considerable acute effects in some animals at very low concentration (Mirocha and Christensen, 1974; Martin and Gilman, 1976; Rukmini and Bhat, 1978).

Screening technique: Before 1977, the search for grain mould resistance was conducted mainly under natural incidence of mould in the field. While this method is

satisfactory in years when the rains are frequent and prolonged throughout the flowering and grain-filling period, it is unsatisfactory when these conditions do not occur and chances of identifying escapes as resistant sources increase (Williams and Rao, 1981). At ICRISAT and Texas A&M, thousands of breeding lines were successfully screened by bagging heads inoculated with conidial-mycelial suspension of *Fusarium moniliforme, Fusarium semitectum* and *Curvularia lunata*, and providing sprinkler irrigation in the evening hours during the grain-filling period. The technique, however, did not work in the extremely hot and dry part of the year (Castor, 1977; Williams and Rao, 1981).

A laboratory-based screening technique was reported by Williams and Rao (1981). They incubated postrainy season grain on blotting paper at 25°C in an alternating 12 h light and 12 h dark regime and were able to distinguish between cultivars in degree of mould development. Anahosur (1983) found that, for screening grain mould resistant sorghums, spray on the panicles after emergence was quite effective for the development of moulds.

Bandyopadhyay and Mughogho (1988) evaluated three techniques for mould screening by inoculating panicles with mould causing fungi, bagging of panicles and providing overhead sprinkler irrigation on rain-free days. They showed that mould resistance screening without inoculation and bagging of panicles was feasible if overhead sprinkler irrigation was used from flowering to harvest (for 54 d from

flowering). When ambient relative humidity was low, however, sprinkler irrigation could also be ineffective in maintaining sufficient humidity for grain mould development. Saikunakorn (1989) showed that inoculation and noninoculation had no distinctive effect on the virulence of the disease. An *in vitro* technique for screening sorghum lines for resistance to *Fusarium moniliforme, Fusarium semitectum* and *Curvularia lunata* was developed by Singh and Prasada Rao (1993). The technique involved inoculation of seeds with the spores of grain mould fungi, transferring inoculated seeds into presterilized petri plates, and incubating at 28°C for 5-6 d in humidity chambers.

Resistant sources: Initially a few resistant sources were reported from natural screening (Gray *et al.*, 1971; Koteswara Rao and Poornachandrudu, 1971) but no information was provided by authors for date of flowering of these resistant sources. Other reports of resistant sources under natural conditions include Zummo (1976), Glueck and Rooney (1976), Rao and Williams (1977), Rana *et al.* (1978), Castor and Frederiksen (1980), Denis and Girard (1980), Pascual and Dalneecio (1985), and Lakshmanan and Mohan (1989). Some of the lines reported as resistant by the above authors are IS 452, IS 455, IS 472, IS 473, Funks 814, E 35-1, IS 2238, IS 2327, IS 14332, IS 2261, IS 9225, CO 25, TNS 25, and TNS 28. Sarwar (1983) screened 26 entries with fungal suspension inoculation and found that IS 14332, Sel-4, Sel-10, IL 8, IL 13 and IL 14 showed least grain mould and greatest germination percentage.

Bandyopadhyay *et al.* (1988) screened 7132 germplasm accessions over several years and identified 156 accessions as resistant. All resistant lines except IS 25017 had coloured pericarp. Coloured lines were of two types, red and brown with a coloured testa. Some of the red resistant sources were IS 14375, IS 14380, and IS 14390. Brown resistant sources included IS 14387, IS 15119, IS 18139, and IS 18240.

Prasada Rao *et al.* (1995) screened 51 photosensitive guinea sorghum germplasm lines using an *in vitro* screening technique and identified 14 accessions showing moderate to high mould resistance.

Singh *et al.* (1995) evaluated 347 converted Zera-zera germplasm accessions against three fungi, *Fusarium moniliforme, F. pallidoroseum* and *Curvularia lunata,* and 143 lines were selected as having moderate to high levels of resistance. Most of these lines mature early, i.e. 29-45 days after flowering.

A large and diverse set of landraces was evaluated for grain mould resistance at different stages of grain maturity (Menkir *et al.,* 1996b). They identified sorghum accessions that were free from colonization by one or more fungal species across three sampling dates. IS 919, IS 2821, IS 3441, IS 9323, IS 9370 and IS 16100 were resistant to *F. moniliforme* for two years across all sampling dates.

Measuring grain moulds: The use of an effective evaluation system is as important as the choice of inoculating technique (Williams and Rao, 1981). Visual assessments of grain mould severity on panicle and seed surface were used for screening resistant sources. Using well-defined units such as percentage of panicle/seed surface affected, field grade score on panicle surface and threshed grade score on seed surface were recorded (Bandyopadhyay and Mughogho, 1988). Mouldiness of the total panicle can be misleading because some cultivars develop mould on the rachis and glumes but maintain clean seed and vice versa (Williams and Rao, 1981). Castor and Frederiksen (1980) noted that field ratings on natural or *Fusarium* inoculated heads would have permitted some susceptible sorghum lines to escape detection, since mould growth on kernels was predominantly hidden by the glumes and became visible only after threshing.

Test weight and germination are two commonly used means of measuring grain mould. In general kernel weight and germination were reduced more by *Fusarium* than *Curvularia* spp. (Castor and Frederiksen, 1980). They also noted that the genotype BTx 398, had little reduction in germination with either *Curvularia* or *Fusarium* infection indicating that the discolouration/mould on kernels was superficial; very little internal damage had occured. Denis and Girard (1977) and Castor and Frederiksen (1980) regarded loss in viability to be so important a part of grain mould that they recommend a germination test as part of standard evaluation for identification of grain mould resistance. Others also found that loss of seed

viability and germination increased with increasing infection by mould causing fungi (Mahalinga *et al.,* 1988; Singh and Agarwal, 1989; Forbes *et al.*, 1989).

Another method of estimating grain mould severity is based on colony-forming units, CFU, or the degree of fungal colonization per unit of kernel tissue. This is measured by serial dilution of dried, ground kernel tissue, plating on selection media, and unting of colonies. Infection frequencies can also be measured by plating and incubating the entire kernel on blotting paper or on a selective agar medium (Hepperly *et al.*, 1982; Gopinath and Shetty, 1985; Granja and Zambolim, 1984; Forbes *et al.*, 1989).

Seitz *et al.* (1977) evaluated grain mould incidence by measuring the concentration of ergosterol (a sterol which is very much specific to fungi and a measure of quantities of total fungal mass present in the seed). Jambunathan *et al.* (1991) studied ergosterol concentration in mould-susceptible and mould-resistant sorghum at different stages of grain development. They found that ergosterol concentration increased with increasing days after flowering in the mould-susceptible accessions and was 10-fold higher in grains collected at 50 days after flowering than in the corresponding mould-resistant accessions. Forbes *et al.* (1989) found that the quantity of ergosterol was highly correlated (r=0.97) to visual grain mould score.

Jambunathan *et al.* (1995) found that concentrations of volatile compounds in mould-susceptible sorghum were higher than those in mould-resistant sorghum. Of the 10 compounds that were identified, 2-methyl butanol was several fold higher in mould-susceptible sorghums.

Seitz *et al.* (1975) measured sprouted kernels, incidence of *Fusarium*, and germination of samples of weathered sorghum in Kansas. It was found that incidence of *Fusarium* was positively related to the amount of sprouting. Hence, a "Fusarium sprouting index" was developed to measure the relative resistance of lines to *Fusarium*-induced sprouting.

Characters associated with resistance: Forbes (1986) reported that on susceptible cultivars initial infection by *F. moniliforme* occurs on the apical ends on the spikelet tissues: lemma, palea, glumes, filaments, and senescing styles. Fungal mycelium advances basipetally, either by colonizing spikelet tissues or by growing in voids between these tissues. Within 5 d of inoculation, mycelium can be seen in all parts of the spikelet, with denser growth around the ovary base. In the next stages of invasion, a dense mycelial mat progresses acropetally, between the aleurone layer and the pericarp. Subsequent invasion of the endosperm, embryonic tissues and pericarp originates from this peripheral mat. Certain plant and grain characteristics are reported to be associated with grain mould resistance (Glueck and Rooney, 1980). Morphological characters like panicle shape, glume, seed size

and days to flower play an important role in governing mould resistance (Glueck *et al.*, 1977). Relative panicle compactness seemed to have little impact on expression of resistance or susceptibility (Williams and Rao, 1981; Ibrahim *et al.*, 1985; Mukuru, 1992; Menkir *et al.*, 1996b).

Differences in maturity can bias mould damage estimates in sorghum. Various studies did not find a strong association between days to 50% flowering and grain mould damage scores (Ibrahim *et al.*, 1985; Mukuru, 1992; Menkir *et al.*, 1996b).

Physical and chemical characters of glumes and seed play an important role in providing resistance against grain mould. The glume appears to be the plant's first defence against fungal invasion; later it is the chemical and physical properties of caryopsis that appear to be more important in resistance to grain moulding (Waniska et al., 1992). Mansuetus *et al.* (1988) found that colony-forming units (CFU) or the numbers of viable fungal propagules were greater on inoculated susceptible cultivars than on resistant ones at the boot leaf stage of growth. Grain mould was negatively correlated with glume cover ($r=-0.56$), glume length ($r=-0.56$) and glume area ($r=-0.62$) when the cultivars were inoculated. The r values were negative and nonsignificant when the cultivars were not inoculated (Mansuetus *et al.*, 1988). Murty (1977) reported that seeds completely enclosed in long papery glumes show resistance to grain mould. Williams and Rao (1980) concluded after examining several thousand diverse sorghum lines at ICRISAT that there was no apparent

correlation between resistance and grain enclosed by long glumes and by normal glumes. Waniska *et al.* (1992) reported relatively high levels of free phenolic compounds (1-2%) in the glumes at anthesis, and their levels increased to 2-10% during normal development. Inoculation with fungi caused an increase in phenolic compounds at 10, 14 and 20 days after anthesis, especially in resistant and moderately resistant cultivars. Mansuetus (1990) found that resistant cultivars responded more to infection than susceptible cultivars by increasing free phenolic compound levels in their glume tissues. They also reported that darker glume colour had increased free phenolic acids and phenolic bound acids than light-coloured glumes.

Physical and chemical properties of the kernel are associated with grain mould resistance (Glueck and Rooney, 1976; Castor and Frederiksen, 1980). In general, darker kernel colour was associated with increased resistance to grain mould (Menkir *et al.*, 1996a; Doherty *et al.*, 1987). It was observed that the pigmented testa was the most influential seed characteristic affecting mould resistance (Ellis, 1972; Esele *et al.*, 1993; Hahn *et al.*, 1983; Hahn and Rooney, 1985; Jimenez and Vallejo, 1986). Waniska *et al.* (1989) reported that cultivars with pigmented testa were more resistant to moulding and contained higher levels of free phenolic acid. Harris and Burns (1973) identified the link between high tannin content and grain mould resistance.

High concentrations of flavan-4-ols have been found to correlate strongly with grain mould resistance (Butler, 1989; Jambunathan *et al.*, 1991; Martinez *et al.*, 1994). Jambunathan *et al.* (1990) found that concentration of flavan-4-ols in grain mould resistant lines was two-fold higher than in mould-susceptible grain at or after 30 days of flowering. Menkir *et al.* (1996b) found that resistant sorghum accessions with red pericarp, but without pigmented testa, had mostly corneous endosperm texture, relatively high levels of apigeninidin, leteolinidin and flavan-4-ols and a negligible amount of tannin. Resistance in this group was strongly associated with high concentration of flavan-4-ols. However, they found an inverse relationship between concentration of flavan-4-ols and resistance to grain mould damage in some red sorghum accessions. Melake-Berhan *et al.* (1996) studied changes in phenolic compounds during seed development. They found flavan-4-ol concentrations were high and similar for both the mould-resistant and mould-susceptible genotypes at early stages of seed development. In susceptible genotypes, the flavan-4-ol concentration dropped by 67% between the third and last sampling dates compared with a 20% decline for the resistant genotypes in the same period. These results indicated that the high flavan-4-ol resistant genotypes, but not the high flavan-4-ol susceptible (hfs) genotypes, maintained high levels of flavan-4-ols throughout seed development and maturation, especially at the time when fungal infection of seeds was at its highest.

Thin mesocarp (thin pericarp) sorghums appeared to withstand weathering better than those with thick mesocarp since thin mesocarp contained few starch granules (Glueck and Rooney, 1980; Rooney and Miller, 1982). Esele *et al.* (1993) observed that when crosses were made between thick mesocarp × thin mesocarp all the progenies in F_1, F_2 and BC_1 were susceptible to grain moulds. This indicated that the factors determining resistance were unrelated to mesocarp thickness.

Sorghum kernels with more corneous endosperm and hard seed were more resistant to grain mould than those with floury endosperm (Ibrahim *et al.*, 1985; Jambunathan *et al.*, 1992; Mukuru, 1992; Garud, 1992; Kumari and Chandrashekar, 1992). These observations led Jambunathan *et al.* (1992) to conclude that grain mould resistance in sorghum cultivars with white pericarp was mostly due to kernel hardness. However Menkir *et al.* (1996a) found that resistance to grain mould was not always associated with the more corneous endosperm texture in white or red pericarp sorghums without pigmented testa. Increased levels of resistance to grain mould in brown sorghums were not associated with endosperm texture. The presence of pigmented testa in brown sorghums confers a greater effect than endosperm texture on reducing grain mould damage (Glueck and Rooney, 1980; Bandyopadhyay *et al.*, 1988; Menkir *et al.*, 1996a).

Glueck and Rooney (1980) found that the most convincing relationships were between resistance and factors affecting water uptake and movement in the grain.

When the moisture content of the grain was at 18 to 20% or more, then microorganism growth was more prolific. Lines with slower drying grain have more mould problems (Williams and Rao, 1980; Singh *et al.*, 1995). Rana *et al.* (1977) studied the water absorption capacity of susceptible and resistant genotypes and found that lines having low water absorption capacity when soaked for a two-hour period, were resistant to grain mould.

Antifungal proteins identified in cereal caryopses such as maize, barley and sorghum were found to play a role in the defence of seeds against pathogen invasion (Vigers *et al.*, 1991; Bass *et al.*, 1992; Kumari and Chandrashekar, 1992; Darnetty *et al.*, 1993). Kumari and Chandrashekar (1994) identified three proteins, with 18, 26, and 30 kDa sizes, that were potentially inhibitory to the growth of *Fusarium moniliforme*, the grain mould pathogen. These proteins appeared only in the endosperm of sorghum grains as revealed by dot immunobinding assay. The 26 and 30 kDa antifungal proteins were also present in pearl millet and maize, while the 18 kDa protein was found only in sorghum. Seetharaman *et al.* (1996) observed significant changes in sorghum antifungal proteins during caryopsis development and post maturation. Sormetin, chitinase and glucanase increased during seed development through physiological maturity (30 days after anthesis) and decreased subsequently. They also found that the levels of antifungal protein were lower in mouldy caryopses from the same panicles, and sormetin levels at 30 days after anthesis correlated significantly with mould ratings ($r=0.65$).

Genetics of resistance: Generation mean analysis of resistance to two grain moulds, namely *C. lunata* and *F. moniliforme,* indicated large dominance effects and significant epistatic effects for resistance. Additive and additive × additive effects were also present but only next in importance to the dominance effects (Murty and House, 1984; Kataria *et al.*, 1990).

Diallel studies of crosses between resistant and susceptible lines under artificial inoculation with fungi indicated that additive gene action was predominant in the inheritance of resistance to *Fusarium* moulds (Narayana and Prasad, 1983) and both additive and non-additive components of variance determined the expression of mould reaction to *Curvularia* (Dabholkar and Baghel, 1983).

Shivanna *et al.* (1994) in their studies with F_1, F_2, BC_1, and BC_2 of crosses between resistant and susceptible lines found that the inheritance of grain mould resistance was governed by four independently assorting genes, two with complementary interactions and the other two with additive interactions.

Patel *et al.* (1983) observed overdominance and partial dominance for grain mould resistance under normal and late sowing conditions.

Esele *et al.* (1993), while studying the genetics of caryopsis traits associated with mould resistance, observed that R-, Y- (pericarp colour) and I- (intensifier) genes

conferred dominant grain mould resistance individually and their effects were additive when present together.

Genetics of associated characters: The open and closed glume character expression indicated its dominance and recessiveness respectively (Singh, 1987). Kullaiswamy and Goud (1982) found that three pairs of genes were involved for gaping glumes, and gaping glumes were dominant over normal glumes.

F_2 segregation for glume colour was found to be 3:1 indicating a single gene difference, reddish purple glume being dominant over blackish-purple glumes (Mani, 1986; Rao and Rana, 1989). Shivanna and Patil (1988), when they crossed black-glumed × straw-glumed lines, found digenic segregation with interaction. Jayaramaiah and Goud (1982) crossed varieties with deep purple coloured glume with light purple coloured glume (ventral side), and found trigenic segregation in F_2 (45:19) with deep purple colour dominant over light purple coloured glume.

Saraswathi *et al.* (1994) found that seed colour was governed by a single dominant gene when red seed was crossed with white seed. Chariya Srichantub (1988) suggested that two genes were involved in the inheritance of phenol content (catechin equivalents).

Genes at seven loci were found responsible for the different characteristics affecting caryopsis traits: R, Y, I, Z, B_1, B_2 and S genes (Stephens, 1946; Quinby and Martin, 1954; Rooney and Miller, 1982). The R and Y genes determine pericarp colour. If both genes are dominant (R-Y-), then the pericarp is red. When the Y gene is homozygous recessive (R-yy or rryy), the pericarp is colourless or white regardless of the R gene. A lemon yellow pericarp is found when the R gene is homozygous recessive and the Y gene is dominant (rrY-). The intensifier gene (I) modifies the colour of the pericarp to appear bright when dominant (I-) and dull when recessive (ii). The B_1 and B_2 genes determine the presence or absence of pigmentation in the testa. When the complementary B_1 and B_2 genes are dominant (B_1-B_2-), testa pigmentation is present, and when either or both genes are homozygous recessive (B_1-b_2b_2, $b_1b_1B_2$-,or $b_1b_1b_2b_2$), pigmentation is absent. The colour of the pigmented testa is controlled by another gene (TP) in which brown is dominant to purple. The spreader gene (S) allows the brown colour of a pigmented testa to be present in the epicarp (S-). The mesocarp is thin when the Z gene is dominant (Z-) and thick when the gene is recessive (zz).

Sorghum genotypes vary in resistance to preharvest sprouting (Clark *et al.*, 1967). In wheat, there are several reports of positive relationship between red seed colour and resistance to sprouting (Gfeller and Svejda, 1960; Khan and Strand, 1977). Reitan (1980) reported two mechanisms for controlling dormancy, one associated with and one not associated with seed coat colour. The mechanism not associated

with seed colour appeared to be contributed by recessive genes in wheat. DePauw and McCaig (1983) found a genetic mechanism for sprouting resistance associated with red colour and one or more mechanisms not associated with seed colour.

Resistance breeding: Initially derivatives of Zera-zera germplasm from Sudan and Ethiopia were used extensively in breeding programmes at ICRISAT and in India to produce high yielding mould tolerant progenies. These progenies were better than the high yielding elite lines for grain mould resistance at low pressure of mould.

Murty *et al.* (1980) utilized 370 parents including Zera-zera and elite lines from national programmes to develop grain mould resistant lines. The F_2 under natural infestation and F_3/F_4 under artificial inoculation were screened to obtain lines less susceptible to *Curvularia* and *Fusarium*. They further reported that increase of level of resistance could be achieved by selective intermating of resistant progenies in specific crosses or recurrent selection in random-mating populations. However, under moderate to high mould disease pressure, these lines became susceptible (Mukuru, 1992). Duncan *et al.* (1987) developed a random-mating population involving 24 experimental or partially converted restorer or maintainer lines chosen for their resistance to *Fusarium* head blight, screened at various locations and developed sources of agronomically desirable B- and R-lines resistant to *F. moniliforme*, *F. semitectum* and *F. roseum*.

Mukuru (1992) developed five white-grained advanced selections with mould resistance by crossing coloured resistant sources with high yielding white susceptible lines after screening the progenies under sprinkler irrigation. He further observed that resistance in white grain type was associated with grain hardness.

Garud *et al.* (1994) developed mould resistant lines *viz.*, GMRP4, GMRP9, GMRP13, GMRP28, GMRP33, by incorporating traits like grain hardness, lax panicle and glume coverage in the breeding programme. Stenhouse *et al.* (1996) mentioned that glume cover and pigmented glume traits have not been fully exploited for development of resistance sources.

Stenhouse *et al.* (1996) reported improvement of guinea sorghum having grain mould resistance through pedigree and population breeding approach to produce high yielding grain-mould resistant guinea material.

Genetics of yield and yield components: Different types of analysis, like diallel, line × tester, and generation mean analysis were conducted on different genotypes for studying the genetics of yield and yield components in sorghum. Additive and non-additive gene actions were significant for variable plant height (Kulkarni and Shinde, 1987; Nimbalkar and Bapat, 1987; Mallick and Gupta, 1988). In some reports, additive gene action was predominant for plant height (Harer and Bapat, 1982; Deshmukh, 1983; Palanisamy and Subramanian, 1986;

Chandrashekharappa, 1987; Yang, 1991; Senthil and Palanasamy, 1994). In contrast, Kide *et al.* (1982), Patil *et al.* (1982), Hugar *et al.* (1986), Berenji (1988), Chhina and Phul (1988), and Wanzel (1988) reported that non-additive gene action was more important for the character.

Predominantly additive gene effect for variable days to 50% flower was observed by Kirby and Atkin (1968), Harer and Bapat (1982), Deshmukh (1983), Kukadia *et al.* (1983), Chandrashekharappa (1987), Mallick and Gupta (1988), and Senthil and Palanasamy (1994). In contradiction, non-additive gene action was found important for days to 50% flower (Kide *et al.*, 1982; Palanisamy and Subramanian, 1986; Wanzel, 1988). Overdominance for the character has also been reported (Anonymous, 1976). Equal importance of additive and non-additive gene effects was reported for flowering by Nagabasaiah (1982), Deshmukh (1983), Hugar *et al.* (1986), Kulkarni and Shinde (1987), and Nimbalkar and Bapat (1987). Nayeem (1991) observed that days to 50% flowering was governed by 13 genes.

Predominantly additive gene effects for panicle length were reported by Patidar and Dabholkar (1981), Harer and Bapat (1982), Nagabasaiah (1982), Patil *et al.* (1982), Thombre *et al.* (1985), Palanisamy and Subramanian (1986), Chandrashekharappa (1987), and Senthil and Palanasamy (1994). Dominance/non-additive gene action was more important than additive gene action for panicle length (Desai *et al.*, 1985; Patil and Thombre, 1985; Chhina and Phul, 1988; Nimbalkar *et al.*, 1988; Wanzel,

1988; Pillai *et al.*, 1995). Partial dominance for this trait was also reported (Anonymous,1976). Both additive and non-additive gene effects were estimated to be important for the character (Giriraj and Goud, 1982; Chandak and Nandanwankar, 1983; Mallick and Gupta, 1988). Among gene interactions, additive × additive was reported to be significant (Karale *et al.*, 1984; Patil and Thombre, 1985; Thombre *et al.*, 1985). Nayeem (1991) reported that the genes involved for panicle length were two to five in number.

Desai *et al.* (1985), Patil and Thombre (1985), Nimbalkar *et al.* (1988), and Rao *et al.* (1994) reported predominantly dominant/non-additive gene effects for primary branches. In contrast, additive gene action for primaries was observed by Indi and Goud (1981a), Thombre *et al.* (1985), and Gao (1992). Importance of both additive and non-additive gene action for this variable was observed by others (Giriraj and Goud, 1982; Hugar *et al.*, 1986; Mallick and Gupta, 1988).

Harer and Bapat (1982), Patil *et al.* (1982), Deshmukh (1983), Thombre *et al.* (1985), Chhina and Phul (1988), Nimbalkar *et al.* (1988), and Rao *et al.* (1994) reported that dominance/non-additive gene effects predominated for panicle weight. Other workers reported additive and non-additive gene action to be important for panicle weight (Giriraj and Goud, 1982; Chandak and Nandanwankar, 1983; Mallick and Gupta, 1988). While Thombre *et al.* (1985), and Rao *et al.* (1994) observed additive × additive gene interaction to be important, Patil and Thombre (1985) and

Nimbalkar *et al.* (1988) found dominant × dominant gene interaction to be more important.

Most workers reported predominantly dominant gene effects for grain yield per plant (Harer and Bapat, 1982; Kide *et al.*, 1982; Nagabasaiah, 1982; Patil *et al.*, 1982; Kukadia *et al.*, 1983; Berenji, 1988; Chhina and Phul, 1988; Yang, 1991; Gao, 1993). In contrast, additive gene action for this trait was reported by Beil and Atkins (1967), Rao *et al.* (1968), Deshmukh (1983), Rao (1970), Patidar and Dabholkar (1981), Giriraj and Goud (1982), Chandak and Nandanwankar (1983), Thombre *et al.* (1985), Shinde and Jagadeshwar (1986), Kulkarni and Shinde (1987), Mallick and Gupta (1988), and Spivakov (1988). Dominance × dominance gene interaction was found to be the most important gene interaction by Indi and Goud (1981a), Indi and Goud (1981b), Desai *et al.* (1985) and Patil and Thombre (1985). Rao et al. (1994) found all three epistatic interactions to be significant in the crosses.

3 MATERIALS AND METHODS

The present study comprised two sets of experiments: The first set dealt with evaluation of sorghum genotypes for grain mould resistance and other related morphological and biochemical characters. The second set involved crossing between susceptible and resistant genotypes selected from the first experiment and analysing the genetic basis of grain mould resistance and related morphological characters.

3.1 EVALUATION OF SORGHUM GENOTYPES FOR GRAIN MOULD RESISTANCE AND RELATED CHARACTERS

Experiments Ia and Ib were conducted during *kharif* 1994 at the Directorate of Oil Seeds, Rajendranagar, Hyderabad (India). Twenty-two sorghum genotypes, including released and prereleased varieties, restorers and nonrestorers, advanced breeding lines, and germplasm lines, obtained from the National Research Centre for Sorghum (NRCS), the All India Co-ordinated Sorghum Improvement Project (AICSIP) and the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) were utilised. The materials utilised in the experiment and ancillary data are listed in Table 2. Seeds of 22 sorghum genotypes were sown in 4 m long rows

Table 2. The sorghum genotypes evaluated for grain moulds during 1994.

S.No	Genotype	Origin	Source	Grain mould resistance*
1	AKMS 14B	India	AICSIP	S
2	296B	India	AICSIP	S
3	AKR 150	India	AICSIP	S
4	MS 422B	India	NRCS	S
5	R 1413	India	NRCS	S
6	IS 14375	Zimbabwe	ICRISAT	R
7	IS 14387	Zimbabwe	ICRISAT	R
8	IS 18144	Lebanon	ICRISAT	R
9	IS 18528	Lebanon	ICRISAT	R
10	IS 24495	S.Africa	ICRISAT	R
11	IS 25017	Sudan	ICRISAT	R
12	SP 33316	India	ICRISRT	MR
13	SP 33349	India	ICRISAT	MR
14	SP 33486	India	ICRISAT	MR
15	GM 15018	India	AICSIP	MR
16	GM 15375	India	AICSIP	MR
17	TNS 30	India	AICSIP	MR
18	B58586	India	AICSIP	R
19	GMRP 13	India	AICSIP	MR
20	IS 21443	Malawi	AICSIP	MR
21	SPV 462	India	AICSIP	S
22	SPV 475	India	AICSIP	S

* S = Susceptible; R = Resistant; MR = Moderately resistant.
AICSIP = All India Coordinated Sorghum Improvement Project, NRCS = National Research Centre for Sorghum, ICRISAT = International Crops Research Institute for the Semi-Arid Tropics.

(two rows each) on ridges 0.75 m apart, in June 1994, in a randomised complete block design in two sets of experiments. Experiment Ia was conducted under sprinklers with three replications for evaluating genotypes for grain mould resistance and other related characters. Experiment Ib was conducted in two replications for recording grain yield per plant and plant height of the genotypes. Standard and recommended agronomical practices were followed throughout the duration of the crop. Land was prepared by deep ploughing, discing and harrowing. Ridging was done 75 cm apart. Atrazine® at a rate of 1 kg ha^{-1} of active ingredient was applied before sowing. A basal fertiliser dose of 42 kg ha^{-1} of N and of P_2O_5 was applied. Seedlings were thinned 20 d after emergence to 10 plants m^{-1} row length. Earthing-up and one hand weeding were done three weeks after emergence. The crop was top dressed with 46 kg ha^{-1} of N 25 d after emergence.

Field screening technique for grain moulds: The screening technique followed was that of Bandyopadhyay and Mughogho (1988). Sprinklers were arranged in sequence grid pattern, the shortest distance between any two sprinklers being 12 m. The test plots were sprinkled for 1h in the morning, if it did not rain the previous night and same morning, and for an additional hour in the evening, if it did not rain throughout the day. Overhead sprinkler irrigation was provided on this basis from flowering to grain maturity (black layer formation) and up to two weeks later when panicles were harvested. Observations were recorded on the following variables.

***Field grade score (FGS)*:** FGS, a visual score for mould severity on the panicle surface, was recorded at the harvesting time. Five panicles from each replication in each test entry were scored visually for mould severity on a scale of 1 = no mould visible on the panicle; 2 = scant superficial mould growth up to 10% of the panicle surface covered by mould; 3 = moderate mould growth and 11-25% of the panicle surface moulded; 4 = considerable mould growth with 26-50% of the panicle surface moulded; and 5 = extensive mould growth with more than 50% of the surface moulded.

Threshed grade score (TGS): TGS estimates the severity of mould effect on the seed surface. Five panicles from each replication of the 22 genotypes were harvested 14 d after maturity (54 d after 50% bloom) and threshed. Each panicle was hand threshed carefully in order to minimise damage to the grain surface. A sample of 35 g of threshed grain was spread in a 9 cm diameter petri plate and scored visually for mould severity. Like FGS, TGS was recorded on 1 to 5 scale, of 1 = no mould and 5 = more than 50% of the seed surface covered by mould.

Grain germination: 100 grains from each of the 5 panicles from each replicate, which were scored for TGR, were incubated in petri dishes lined with wet filter paper, for 4 d at 30°C, and number of germinated seed was counted.

Ergosterol: Ergosterol was determined according to the modified method of Jambunathan *et al.* (1991). From each entry, 3 panicles were chosen at random and dried. Grains from dried panicles were removed and mixed thoroughly. A 25 g sample of the mixed grain was ground in a Udy Cyclone mill (U.D. Corp., Boulder, CO) to pass through a 0.4 mm screen. Duplicate 10g of samples of ground grain were weighed in polythene screw cap bottles (125 ml capacity), 50 ml of methanol (MeOH) was added, and bottles were shaken vigorously on a reciprocating shaker for 60 min at room temperature. The mixture was allowed to settle and 25 ml of clear extract was transferred into a screw-capped test tube containing 3 g of KOH and was shaken till the KOH dissolved. Ten millilitres of n-hexane was added and the mixture was incubated at 75°C in a water bath for 30 min and then allowed to cool to room temperature. Five ml of distilled water was then added, the solution was mixed thoroughly, and the top hexane layer was removed with the help of Pasteur pipette and transferred to a 50 ml beaker. To the remaining aliquot in the test tube, 10 ml of hexane was added and mixed vigorously and hexane layer was removed carefully and pooled with the earlier extract. This procedure was repeated twice and all the pooled hexane extracts in the beaker were evaporated to dryness in a hot-water bath. The residue was redissolved in 5 ml methanol (HPLC grade) and filtered through a 0.45 mm filter (Millex, HV, Millipore Corp., Bedford, MA) and the filtrate was used for ergosterol analysis.

Ergosterol was determined in a SHIMADZU LC-6A high performance liquid chromatograph with manual loading. The extract was loaded on a reverse-phase column [3 µm particle size, 6 mm × 8 cm] consisting of two 4 cm Zorpax Reliance Cartridges (DuPont). The mobile phase was methanol-water (96:4 v/v) at a flow rate of 1.2 ml min^{-1}. The column temperature was maintained at 50°C, and the absorbance of eluted ergosterol was detected at 282 nm. The standard ergosterol (Sigma) had a retention time of 8.3 min.

Along with the experimental sample, a sample of standard grain mould susceptible check variety (Bulk Y) was also analysed every time to maintain the accuracy of the procedure. The standard ergosterol was loaded in 2.5, 5.0, 7.5, and 10.0 mg concentration for computation of the instrument every time. The instrument was calibrated for standard ergosterol and directly gave ergosterol content of the sample in ppm.

Estimation of total phenols: The Folin-Ciocalteau's method (Kaluza *et al.*, 1980) was followed for estimation of total phenols in glumes and seeds of sorghum. Developing sorghum panicles were tagged at 50% flowering and harvested 30 d after flowering. At each time of sampling, three panicles from each replicate were collected and oven dried soon thereafter. Glumes from oven dried panicles were removed and were mixed thoroughly. About 2 g of glume sample was ground in a Udy Cyclone mill to pass through a 0.4 mm screen.

Similarly, seeds were collected from three panicles from each replication 40 d after flowering, oven dried and mixed thoroughly. About 2 g of seed was ground in Udy Cyclone mill. The glume and seed powder were defatted with n-hexane and air dried. Duplicate 250 mg samples of defatted glume and seed material were extracted twice with 5 ml methanol and twice with 5 ml methanol-HCl (1NHCL). Tubes containing the defatted glume and seed material suspended in the extractant were placed on Staurt tube rotator (TR-2) and mixed for 1 h. The tubes were then centrifuged for 10 min and the supernatant decanted into vials. The two methanol extracts for each sample and the two methanol-HCl extracts were pooled separately to form methanol and acid-methanol extracts.

One ml of methanol extract and 1 ml acid-methanol extract were mixed in a 50 ml volumetric flask. One ml of 1N Folin-Ciocalteau's reagent (diluted 2N Folin-Ciocalteau's reagent to 1N with water) and 2 ml of 20% sodium carbonate solution were added to the extract and mixed. The flasks were incubated for 15 min in a water bath at 60°C then removed and cooled to room temperature. Volume was made up to 50 ml by adding distilled water. Readings for absorbance were recorded at 560 nm against reagent blank.

One mg of tannic acid was dissolved in 1 ml water and 0.2, 0.3, 0.4, and 0.5 ml aliquots made up to 1 ml with methanol. The procedure given above for analysis of

phenols was followed and a standard curve was plotted. Using the standard curve, the quantity of phenol as mg tannic acid equivalent (g sample)$^{-1}$ was calculated.

Estimation of flavan-4-ols: The procedure of Butler (1982) was followed for estimation of flavan-4-ols in glumes and seeds. 0.5 ml of the methanol-HCl extract, prepared as described above, was taken and 7 ml of water-saturated butanol was added. Simultaneously a blank was prepared by mixing methanol, water-saturated butanol and 0.1N acetic acid in a 70:15:15 ratio v/v. The tubes along with the blank were rotated in the test tube rotator for 1 h. The absorbance was read at 550nm in spectrometer (spectronic 21, Bausch & Lamb, USA). All the results were calculated as A 550 g^{-1} dry sample.

Seed hardness: Seeds were equilibrated to a moisture content of 6.5 ± 1.0% by keeping the samples in the oven at 37°C for 3-4 d, before hardness determinations were made. The seed hardness was tested by measuring resistance to grinding by the Stenvert hardness tester (Glencreston, Stanmore, England). The grinding resistance offered by 18 g of sorghum grains in a micro hammer-cutter mill was measured in seconds to obtain a fixed volume of flour (Pomeranz *et al.,* 1985).

Number of days to flowering: In different genotypes, flowering data were recorded on ten random panicles in each replication. Also days to 50% flowering was recorded in each panicle.

***Plant height and grain yield per plant*:** In experiment Ib, data on plant height (cm) and grain yield per plant (g) were recorded on 10 random plants in two replications.

Percentage glume cover: Percentage seed cover by glume was recorded visually as 25% glume cover, 50% glume cover, 75% glume cover, 90% glume cover and 100% glume cover.

Glume colour: Visual scores of 1 to 5 were given to different glume colours, where 1 = straw glume, 2 = light red glume, 3 = red glume, 4 = dark purple glume; and 5 = black glume.

Seed colour: Visual scores given to seed colour were 1 = white seed, 3 = red seed, and 5 = brown seed.

***Glume index*:** Glume index (GI) was calculated as given below.

GI = Length of glume/breadth of glume.

Means, coefficients of variation (CV), standard errors (SE) and correlations were calculated using the GENSTAT 5 statistical package. Correlations were estimated between Field Grade Score, Threshed Grade Score, and different biochemical and morphological characters.

3.2 GENETICS OF GRAIN MOULD RESISTANCE AND RELATED CHARACTERS

During *kharif* of 1995 and 1996, 10 and 8 crosses, respectively, were made between mould resistant and susceptible genotypes. A list of the genotypes selected for crossing and different cross combinations is given in Table 3. The F_1 hybrids and the parent lines were raised during *rabi* 1994 and 1995 and additional crosses were made to generate 6 families *viz.*, P_1, P_2, F_1, BC_1, BC_2, and F_2 in each cross. Six families in each of the 10 and 8 crosses were grown during *kharif* 1995 and 1996, respectively, at ICRISAT Asia Center, Patancheru, Andhra Pradesh. These families were grown in a randomised complete block design with three replications on 4 m long ridges 0.75 m apart. Each parental line, F_1, BC_1 and BC_2, was grown in a single-row plot and F_2s were grown in 4-row plots. The experimental materials were screened for grain mould resistance under sprinkler irrigation as described above.

During 1996, replicated yield trials of families from two crosses of grain mould susceptible × resistant varieties were grown for genetic analysis of grain yield and yield components, and their relation to other traits. The families, in each cross, were grown in a randomised complete block design with two replications on 4 m long ridges 0.75 m apart. Parental lines, F_1s, BC_1s and BC_2s had a single-row plot and F_2s had 4-row plots. In each replication observations were recorded on ten plants

Table 3. Parents used in crosses for generation mean analysis experiments during 1995-96.

Genotype	Symbol	Pedigree/Origin	Sources	Disease reaction*	Traits** GCCL	SDCL	SDTEX	List of crosses made (1995)	(1996)
MS 422B	S_1	SPV 422 x 2219B	NRCS	S	C	W	Sf	$S_1 \times R_1$	$S_1 \times R_1$
SP 33316	S_2	ICSB 11 x IS 2815	ICRISAT	S	C	W	Sf	$S_2 \times R_1$	$R_1 \times R_2$
GM 15018	S_3	IS 25017 x ICSR38	ICRISAT	S	C	W	Sf	$S_3 \times R_2$	$R_2 \times R_3$
AKMS 14B	S_5	India	AICSIP	S	St	W	Sf	$S_5 \times R_1$	$S_5 \times R_1$
AKR 150	S_6	India	AICSIP	S	St	W	Sf	$S_6 \times R_1$	-
IS 14375	R_1	Zimbabwe	ICRISAT	R	C	C	Hd	$S_1 \times R_2$	$S_1 \times R_2$
IS 14387	R_2	Zimbabwe	ICRISAT	R	C	C	Hd	$S_2 \times R_2$	-
IS 25017	R_3	Sudan	ICRISAT	R	C	W	Hd	$S_1 \times R_3$	$S_1 \times R_3$
IS 30469-6-1518-2	R_6	India	ICRISAT	MR	St	W	-	$R_1 \times R_2$	$S_1 \times R_6$
IS 24495	R_{16}	S.Africa	AICSIP	MR	St	W	Hd	$R_2 \times R_3$	$S_1 \times R_{16}$

* S = Susceptible; R = Resistant; MR = Moderately resistant.
** GCCL = Glume colour, C = Coloured glume, St = Straw glume; SDCL = Seed colour, W = White seed, C = Coloured seed; SDTEX = Seed texure, Sf= Soft seed and Hd = Hard seed.
NRCS = National Research Centre for Sorghum, ICRISAT = International Crops Research Institute for the Semi-Arid Tropics, AICSIP = All India Coordinated Sorghum Improvement Project.

each from P_1, P_2 and F_1, 15 plants each from BC_1 and BC_2, 70 to 75 plants from F_2 in 1995 and 65 plants from F_2 in 1996. Data on the following traits were recorded.

Field grade score: Panicles from different families and crosses were scored visually for mould severity 54 d after 50% flowering. FGS was recorded on a scale of 1 to 9 where, 1 = free from mould, 2 = 5% of the panicle moulded, 3 = 10% of the panicle moulded, 4 = 15% of the panicle moulded, 5 = 30% of the panicle moulded, 6 = 40% of the panicle moulded, 7 = 50% of the panicle moulded, 8 = 60% of the panicle moulded and 9 ³ 70% moulded.

Threshed grade score: The panicles which were evaluated for FGS were harvested and threshed carefully. Samples of 35 g of seed from each panicle were spread on petri dishes and were scored visually for mould severity on the seed surface on a scale of 1 to 9 as described for FGS.

Number of days to flower: Flowering data were recorded on individual plants from each family in each cross. Also data on days to 50% anthesis were recorded.

Seed colour: During 1995, seed colour was scored on a scale of 1 to 10 in all the crosses except white seed × white seed ($S_1 \times R_1$); 1 = white, 2 = grey, 3 = very light red, 4 = light red, 5 = red, 6 = yellow, 7 = light brown, 8 = brown, 9 = dark brown, and 10 = reddish brown.

Percentage glume cover: Percentage seed cover by glume was scored as described above.

Percentage sprouting on panicle: Percentage preharvest sprouting (0 to 100%) was estimated visually on panicle during 1995.

Glume colour: During 1995, the cross between straw glume (S_s) × purple glume (R_1) was scored at the time of harvesting on a scale of 1 to 9; where 1 = straw, 2 = grey, 3 = light red, 4 = red, 5 = light brown, 6 = purple, 7 = dark purple, 8 = black, and 9 = dark black glume.

Grain yield and yield components: Yield and yield components *viz.*, plant height, panicle length, panicle weight, primary branches and yield per plant were recorded in the two crosses, $S_1 \times R_1$ and $S_1 \times R_2$, grown in the yield trial experiment. Means, SEs, and variances of the families were estimated in different crosses. In different crosses frequency distributions of all the families were worked out.

***Generation mean analysis*:** Generation mean analyses were carried out on original and where necessary on transformed data. Square root transformation was applied to the variables FGS and TGS, and angular transformation was applied to the variables percentage sprouting and percentage glume cover. Genetic effects of the generation means were estimated by a weighted least square regression

(WLSR) analysis (Cavalli, 1952; Hayman,1958) using the notation and definition of Mather and Jinks (1977; pp 36-67).

Since generation means of parents and progenies were estimated with equal percision, each generation was weighted by the variance of the mean for that generation. The equation fitted for Least Square Regression was

$$\underset{\sim}{Y} = \underset{\wedge}{X}\,\underset{\sim}{B} + E$$

$\underset{\sim}{Y}$ = Vector of generation means = [P_1, P_2, F_1, F_2, BC_1, BC_2]'

$\underset{\wedge}{X}$ = Coefficient matrix

$\underset{\sim}{B}$ = Vector of parameter = [m d h i j l]'

E = Enov vector

Where m = mean, d = additive effects, h = dominance effects, i = additive × additive interactions, j = additive × dominance interactions, l = dominance × dominance interactions.

The coefficient matrix is

Generations Parameters

	[m]	[d]	[h]	[i]	[j]	[l]
P_1	1	1.0		1.00		
P_2	1	-1.0		1.00		
F_1	1		1.0			1.00
F_2	1		0.5			0.25
BC_1	1	-0.5	0.5	0.25	-0.25	0.25
BC_2	1	-0.5	0.5	0.25	-0.25	0.25

stimates of genetic parameters were derived from the equation

$\underset{\sim}{B}$ $= (X^T W^{-1} X)^{-1} (X^T W^{-1})Y$

Where X^T = Transpose of X

$\underset{\sim}{B}$ = Vector of estimates of parameter

W = Diagonal matrix for weights

$= diag[s^2_{P1}, s^2_{P2}, s^2_{F1}, s^2_{BC1}, s^2_{BC2}, s^2_{F2}]$

W^{-1} = Inverse of weight matrix, W

Suitability of the genetic model was judged by its R^2 value and by the model-associated F-statistic which indicates whether a statistically significant relationship exists between the genetic effects and the genetic means. Significance of estimates of genetic parameters were tested by t-test. Step-wise regression was followed in an attempt to obtain the best possible regression for the given set of response and explanatory variables. Initially the method starts by fitting a one-term model by introducing the variable that had largest correlation with the response variable. Subsequently, it adds new variable which has largest partial F-statistic or which minimized the residual mean squares or improves R^2. At each stage it tries to avoid a variable or drop a variable whichever improves R^2. The current model is modified by the best term according to the criteria based on variance ratio. Suppose that the residual sum of squares and residual degrees of freedom for current model are S_0 and D_0 and after making a one-term change S_1 and D_1. If the variance ratio for any term that is dropped is greater than the value of a preset outratio, the term that most reduces residual mean square is dropped i.e., a term is dropped if at least one

term has

$[(S_1-S_0)/(D_1-D_0)] / (S_0/D_0) >$ Outratio

If no term satisfies the criteria for dropping, then the term that most reduces the residual mean square is added to the model if the variance ratio is

$$[(S_0-S_1)/(D_0-D_1)] / (S_1/D_1) > \text{Inratio}$$

If neither criterion is met, the model is left unchanged and is deemed as the optimal model. Generally outratios and inratios are taken to be 4, which corresponds roughly to the upper 5% point of the F distribution. For the variables, seed colour, percentage glume cover and percentage sprouting, observations recorded from some generations were constant and hence the variances were zero. The usual weights for these variables will be infinite, so normal scaling test cannot be applied. Hence unified theory of least square (Rao, 1973) was used for estimating these parameters.

Similarly estimates of genotype x environment interactions were calculated by weighted least square regression analysis as described above, on the two years pooled data of six crosses.

The coefficient matrix for genotype × environment:

Generations	Years	Parameters					
		[m]	[d]	[h]	[e]	[exd]	[exh]
P_1	1995	1.0	1.0		1.0	1.0	
P_1	1996	1.0	1.0		-1.0	-1.0	
P_2	1995	1.0	-1.0		1.0	-1.0	
P_2	1996	1.0	-1.0		-1.0	1.0	
F_1	1995	1.0		1.0	1.0		1.0
F_1	1996	1.0		1.0	-1.0		-1.0
BC_1	1995	1.0	0.5	0.5	1.0	0.5	0.5
BC_1	1996	1.0	0.5	0.5	-1.0	-0.5	-0.5
BC_2	1995	1.0	-0.5	0.5	1.0	-0.5	0.5
BC_2	1996	1.0	-0.5	0.5	-1.0	0.5	-0.5
F_2	1995	1.0		0.5	1.0		0.5
F_2	1996	1.0		0.5	-1.0		-0.5

Where m = mean, d = additive effects, h = dominance effects, e = environment effects, exd = environment × additive interactions, exh = environment × dominance interactions.

Results

4 RESULTS

4.1 PERFORMANCE OF SORGHUM GENOTYPES FOR GRAIN MOULD RESISTANCE AND MORPHOLOGICAL CHARACTERS

A list of the 22 genotypes studied with ancillary data is given in Table 2. The means of these genotypes for different variables recorded are summarised in Table 4.

4.1.1 Means

Field Grade Score (FGS): The various genotypes screened under sprinkler irrigation recorded mean scores of 1 to 5 for FGS. The genotypes, IS 14375, IS 14387, IS 18144, IS 18528, IS 24495, IS 25017, SP 33487, and B58586, recorded mean FGS scores of 1.3 to 3.0 and thus were classified as resistant (Plate 2). The genotypes, 296B, SPV 475, SPV 462, MS 422B, AKMS 14B, AKR 150, and R 1413, showed mean FGS scores of 4 to 5 and were considered as susceptible (Plate 3). The remaining 7 genotypes gave moderate FGS mean scores of 3.1 to 3.9 and were considered as moderately resistant.

Threshed Grade Score (TGS): Means of the genotypes screened for this variable ranged from 1.9 to 5. Genotypes, viz., 296B, SPV 462, SPV 475, MS 422B, AKMS 14B, AKR 150, R 1413, SP 33487, GM 15373, TNS 30 and GMRP 13 with mean

Table 4. Means of different variables in 22 sorghum genotypes.

Genotype	FGS	TGS	%GER	ERGO (µg/g)	G-PHEN	G-PHEN*	S-PHEN	S-PHEN*	G-FLAV (A550.g-1)	S-FLAV (A550g-1)
ASMS 14B	4.9	4.9	28.3	70.8	113.3	70.0	41.7	66.7	0.0	0.0
296B	5.0	5.0	6.4	253.6	73.3	81.7	40.0	36.7	0.0	0.0
AKR 150	4.6	4.7	35.4	170.1	106.7	90.0	76.7	86.7	0.0	0.0
MS 422B	4.8	4.7	52.9	92.3	216.7	186.7	116.7	91.3	0.0	0.0
R 1413	4.6	4.8	18.3	134.0	166.7	116.7	73.3	83.3	0.0	0.0
IS 14375	1.4	1.9	89.5	13.9	123.3	186.7	160.0	166.7	0.1	0.1
IS 14387	1.6	1.9	94.7	5.7	146.7	240.0	333.3	230.0	0.0	0.0
IS 18144	2.0	2.2	90.3	10.9	200.0	233.3	580.0	175.0	0.1	0.1
IS 18528	2.4	2.5	83.8	17.6	170.0	203.3	288.3	200.0	0.3	0.3
IS 24495	3.0	3.1	80.6	12.3	116.7	130.0	74.0	80.0	0.0	0.0
IS 25017	2.8	3.0	89.3	44.5	143.3	100.0	76.7	76.7	0.0	0.0
SP 33316	3.2	3.3	68.3	40.9	216.7	216.7	53.3	90.0	0.2	0.0
SP 33349	3.1	3.6	77.8	16.0	310.0	223.3	126.7	126.7	0.2	0.2
SP 33487	2.7	4.5	45.9	38.6	310.0	216.7	176.7	180.0	0.0	0.0
GM 15018	3.1	3.5	63.4	55.5	200.0	166.7	51.7	60.0	0.0	0.0
GM 15373	3.6	4.2	34.8	29.9	176.7	151.7	86.7	96.7	0.0	0.0
TNS 30	3.7	4.2	57.4	45.2	193.3	116.7	90.0	93.3	0.0	0.0
B58586	2.7	3.0	84.2	25.1	46.7	33.3	76.7	76.7	0.0	0.0
GMRP 13	3.8	4.7	27.2	109.8	150.0	151.7	60.0	66.7	0.0	0.0
IS 21443	3.1	3.3	85.4	34.4	63.3	43.3	46.7	75.0	0.0	0.0
SPV 462	4.8	5.0	44.6	102.4	96.7	103.3	63.3	121.7	0.0	0.0
SPV 475	4.5	4.9	21.8	177.9	173.3	136.7	58.3	80.0	0.0	0.0
Mean	3.4	3.8	58.2	68.2	159.7	144.2	125.0	107.3	0.0	0.0
SE±	0.1	0.1	6.1	19.0	20.3	23.5	17.8	19.4	0.0	0.0
CV(%)	6.8	7.4	18.3	48.4	22.0	28.2	24.7	31.4	62.8	50.3

FGS = Field grade score, TGS = Threshed grade score, %GER = Germination, ERGO = Ergosterol, G-PHEN = Glume phenol, G-PHEN* = Glume phenol in acid methanol, S-PHEN = Seed phenol, S-PHEN* = Seed phenol in acid methanol, G-FLAV = Glume flavan-4-ols, S-FLAV = Seed flavan-4-ols, S-HRD = Seed hardness, DF = Days to flower, HT = Plant height, YD/PL = Yield/plant, %G-COV = Glume cover, GLCL = Glume colour, SDCL = Seed colour, GLINDX = Glume index

Table 4 Contd...

Genotype	S-HRD (Sel)	DF (see)	HT (cm)	YD/PL (g)	%G-COV	GLCL	SDCL	GLINDX
ASMS 14B	4.17	56	139.0	56.0	25.0	1	1	1.5
296B	3.05	66	129.0	70.5	25.0	1	1	1.1
AKR 150	3.61	60	141.8	72.2	50.0	1	1	2.2
MS 422B	4.55	61	155.7	79.2	50.0	4	1	2.6
R 1413	3.98	72	152.1	74.2	25.0	1	1	2.6
IS 14375	6.47	69	295.3	59.6	50.0	5	3	1.6
IS 14387	6.78	61	250.1	56.4	50.0	5	5	2.4
IS 18144	4.65	59	222.3	39.7	75.0	5	3	2.5
IS 18528	5.07	58	203.4	37.4	75.0	5	5	2.5
IS 24495	5.39	51	217.8	29.7	25.0	1	1	2.0
IS 25017	5.70	73	285.6	78.5	50.0	5	1	1.6
SP 33316	4.90	60	178.3	59.3	25.0	3	1	1.6
SP 33349	5.66	58	176.0	52.8	50.0	3	3	1.5
SP 33487	4.05	62	132.5	77.5	50.0	2	5	1.6
GM 15018	4.59	59	163.4	90.0	25.0	2	1	1.3
GM 15373	4.96	57	159.2	51.7	25.0	4	1	1.3
TNS 30	4.28	69	215.0	69.2	50.0	1	1	1.0
B58586	6.04	67	295.5	59.8	50.0	1	1	2.0
GMRP 13	3.79	70	218.8	92.3	40.0	1	1	1.6
IS 21443	5.16	63	265.6	49.7	90.0	1	1	1.3
SPV 462	4.22	70	237.0	106.7	25.0	1	1	1.6
SPV 475	3.09	70	194.9	84.8	50.0	1	1	1.3
Mean	4.73	63	201.3	66.3	44.1	2.3	1.6	1.8
SE±	0.36	1	11.2	6.5	4.0	0.4	0.3	0.1
CV(%)	13.30	3	7.9	13.9	42.2	73.3	79.0	28.9

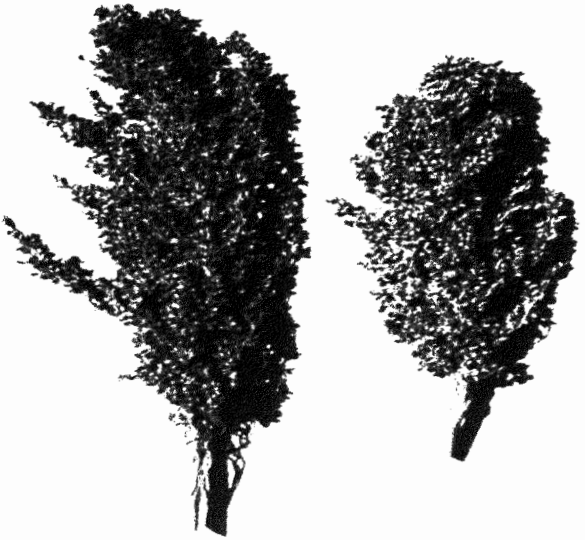
FGS = Field grade score, TGS = Threshed grade score, %GER = Germination, ERGO = Ergosterol, G-PHEN = Glume phenol, G-PHEN* = Glume phenol in acid methanol, S-PHEN = Seed phenol, S-PHEN* = Seed phenol in acid methanol, G-FLAV = Glume flavan-4-ols, S-FLAV = Seed flavan-4-ols, S-HRD = Seed hardness, DF = Days to flower, HT = Plant height, YD/PL = Yield/plant, %G-COV = Glume cover GLCL = Glume colour, SDCL = Seed colour, GLINDX = Glume index

Plate 2. Panicles of grain mould resistant sources.

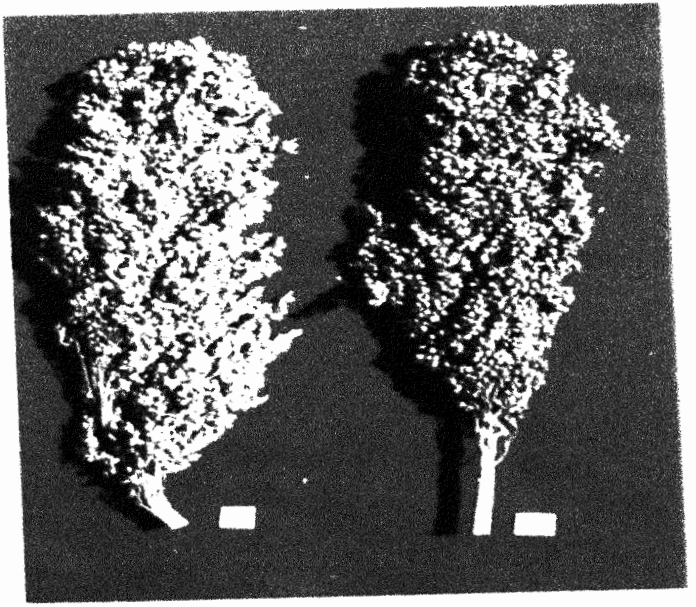
A: coloured grain sources; R1 = IS 14375 , R2 = IS 14387.

B: White grain sources; R7 = B58586, R8 = IS 21443.

Plate 2



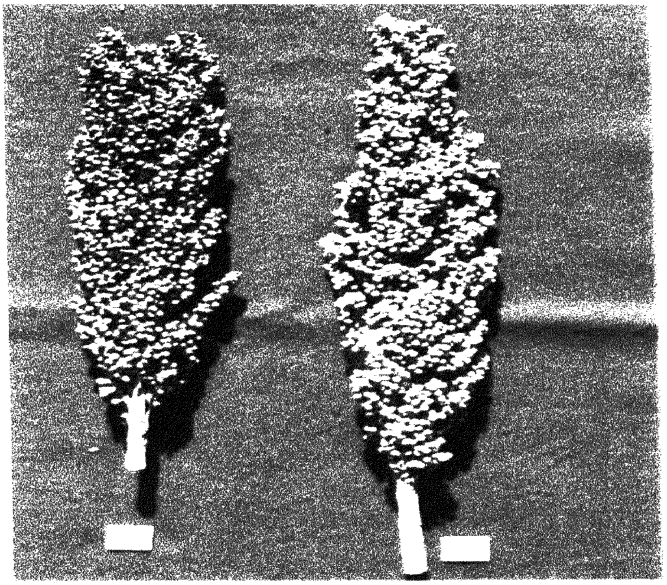
A

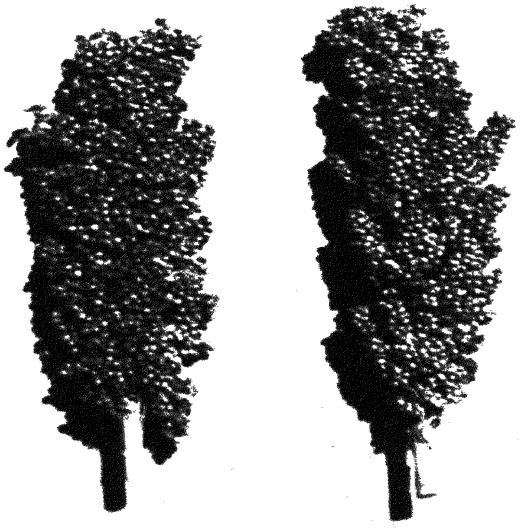


B

Plate 3. Panicles of grain mould susceptible sources; S_1 = AKMS 14B, S_2 = MS 422B, S_3 = R 1413, S_4 = AKR 150.

Plate 3



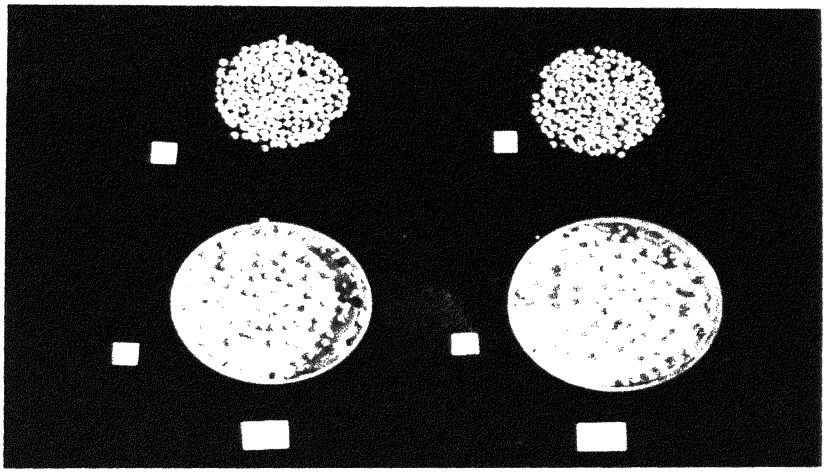


TGS of 4 to 5 showed maximum susceptibility to grain mould. On the other hand, IS 14375, IS 14387, IS 18144, IS 18528, IS 25017, B58586, and IS 21443, recorded mean TGS of 1.9 to 3, exhibiting high resistance to grain moulds.

Germination percentage (%GER): Means for seed germination varied from 6 to 94% with 296B being most affected by grain moulds and recording least (6%) seed germination (Plate 4). The genotypes with coloured grain, *viz.*, IS 14375, IS 14387, IS 18144, and IS 18528, showed high mean %GER, indicating negligible damage caused by grain moulds (Plate 5). White grain lines, IS 25017, IS 24495, IS 21443 and B58586, also showed high mean seed germination (80 to 90%) although some of them showed moderate mean values for FGS and TGS.

Ergosterol (ERGO): The mean quantity of ergosterol in different lines ranged from 5 to 253 mg gseed^{-1}. The line 296B showed maximum ERGO content of 253 mg gseed^{-1} while IS 14387 had minimum content of 5 mg gseed^{-1}. Fig. 1 depicts chromatographs indicating the different quantities of ERGO in susceptible and resistant genotypes. Genotypes IS 14375, IS 14387, IS 18144, IS 18528, IS 24495, IS 25017, B58586 and IS 21443, recorded low ERGO contents of 5 to 45 mg gseed^{-1}. On the other hand, genotypes 296B, SPV 462, SPV 475, AKR 150, MS 422B and AKMS 14B, recorded high ERGO contents ranging from 70 to 253 mg gseed^{-1}.

Plate 4



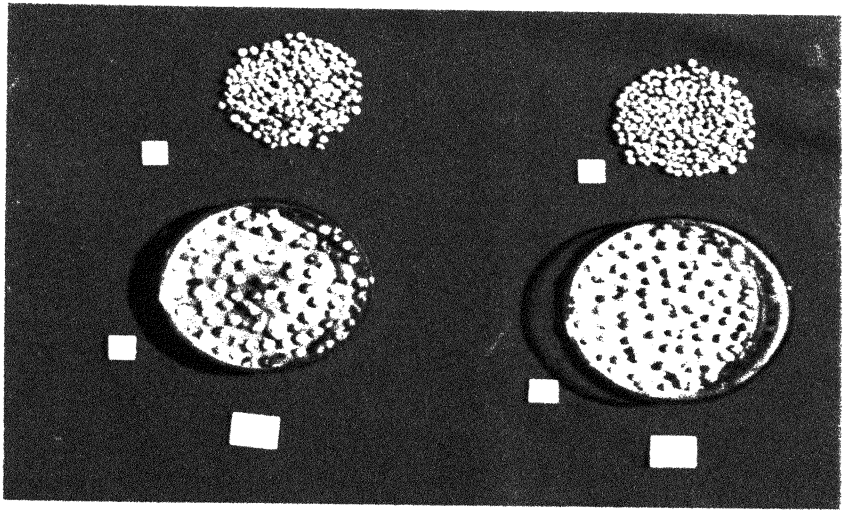
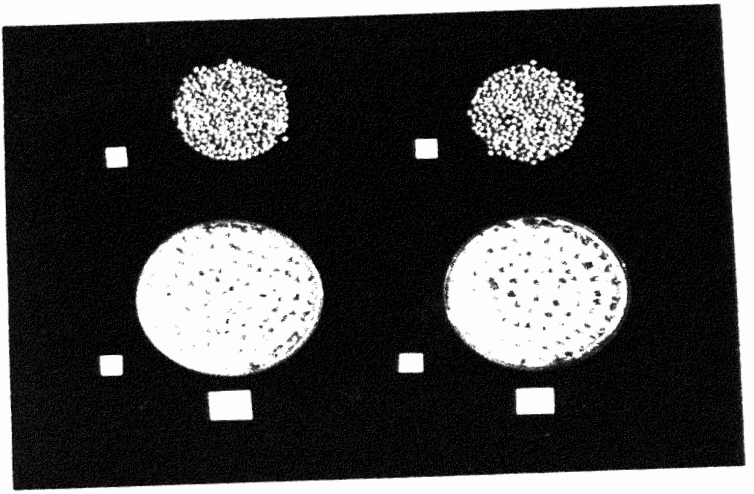
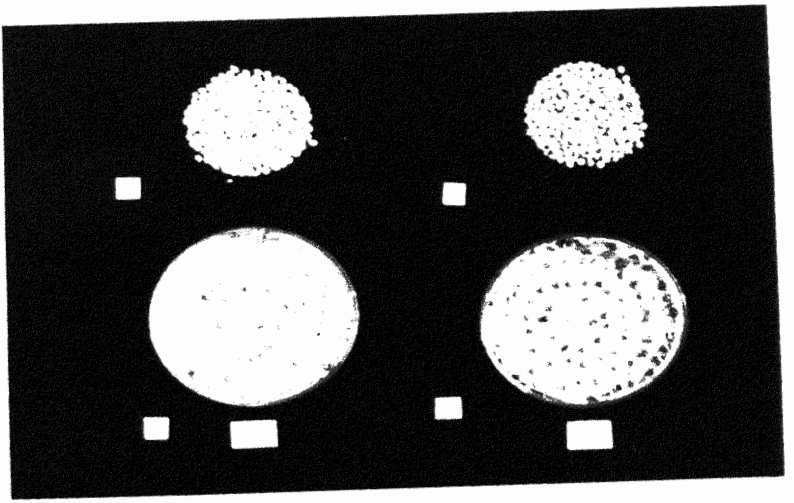
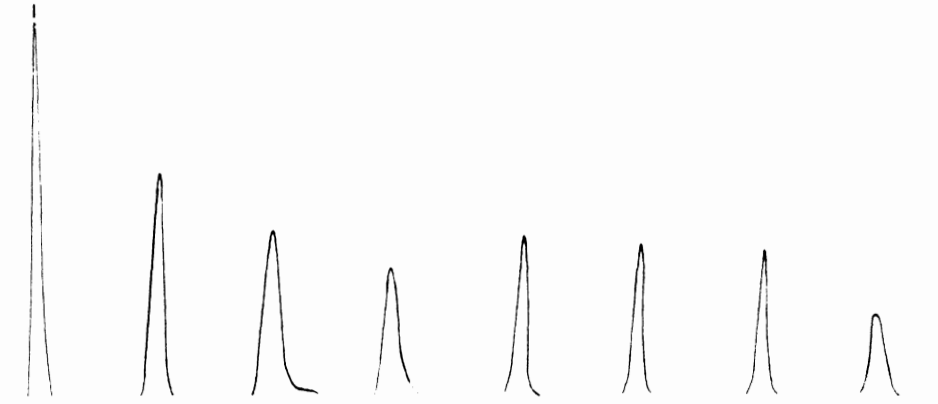


Plate 5. Seed and germination in grain mould resistant parents. R_1 = IS 14375, R_2 = IS 14375, R_7 = B58586 and R_8 = IS 21443. a = Seed, b = Seed germination.

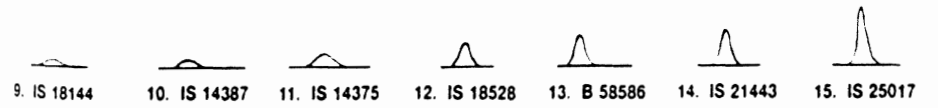
Plate 5







A: Susceptible Lines (1 to 8):



B: Resistant Lines (9 to 15):

Fig 1 Chromatograms of ergosterol in grain mould susceptible and resistant lines of sorghum.

Glume phenols: In different genotypes glume phenols in methanol extracts (G-PHEN) and acid-methanol extracts (G-PHEN^{+}) ranged from 33 to 310 mg gseed^{-1}. The line SP 33487 recorded the maximum phenol content of 310 mg gseed^{-1}, while B58586 recorded the minimum content of 33 mg gseed^{-1}. Eight lines, *viz.*, SP 33349, SP 33487, SP 33316, IS 14387, IS 14375, IS 18144, IS 18528, and GM 15018, were characterised by high phenol contents of 123 to 310 mg gseed^{-1}. Other lines, 296B, SPV 462 and IS 21443, showed moderate phenol content of 40 to 100 mg gseed^{-1}.

Seed phenols: The lines showed wide variation for seed phenols in both methanol (S-PHEN) and acid-methanol (S-PHEN^{+}) extracts ranging from 36 to 580 mg gseed^{-1}. The genotype IS 18144 showed the maximum seed phenol content of 580 mg gseed^{-1}, while 296B showed the least content of 36 mg gseed^{-1}. Certain other lines, *viz.*, IS 14375, IS 14387, IS 18144, IS 18528, and SP 33487, showed high content of seed phenols ranging from 160 to 580 mg gseed^{-1}.

Glume flavan-4-ols (G-FLAV): In a very few genotypes, *viz.*, IS 14375, IS 18144, IS 18528, SP 33316 and SP 33349, glume flavan-4-ols were detected. The line IS 18528 recorded the highest level of glume flavan-4-ols.

Seed flavan-4-ols (S-FLAV): Except SP 33316, all other lines having G-FLAV also developed flavan-4-ols in their seeds. Here also IS 18528 recorded the highest content of seed flavan-4-ols.

Seed hardness (S-HRD): The seed of various genotypes, harvested from *kharif* crop, took 3.0 to 6.78 sec to grind a standard volume. Eight lines, IS 14375, IS 14387, IS 18528, IS 24495, IS 25017, SP 33349, B58586 and IS 21443, were relatively hard seeded taking 5 to 6 sec to grind, while 296B and SPV 475 took only 3 sec to grind.

Days to flower (DF): Among genotypes DF varied from 51 to 73 days to reach 50% flowering. Lines IS 24495, AKMS 14B, IS 18144, IS 18528, SP 33316, SP 33349, GM 15018 and GM 15373, were found early flowering (51 to 60 days), and MS 422B, IS 14387, SP 33487, and IS 21443, were medium flowering (61 to 65 days); whereas 296B, R 1413, IS 14375, IS 25017, GM 15373, B58586, SPV 462 and SPV 475, were late flowering (66 to 73 days).

Plant height (HT) and grain yield plant^{-1} (YD/PL): Plant height of the genotypes ranged from 129 to 295 cm and the grain yield varied from 29 to 106 g plant^{-1}. Grain yields of SPV 462, SPV 475, 296B, AKR 150, MS 422B, R1413, IS 25017, SP 33487, GM 15018 and GMRP 13, were very high ranging from 70 to 106 g plant^{-1}.

Glume cover (% G-COV): Glume cover on the seed varied from 25 to 90%. Three lines, IS 21443, IS 18144, and IS 18528, showed maximum glume cover of 90%, 75% and 75% respectively, on the seed.

Glume colour (GL- CL): Eleven genotypes, AKMS 14B, 296B, AKR 150, R 1413, IS 24495, TNS 30, B58586, GMRP 13, IS 21443, SPV 462 and SPV 475, had straw-coloured glumes (score 1), while seven genotypes, MS 422B, IS 14375, IS 14387, IS 18144, IS 18528, IS 25017 and GM 15373, showed dark glumes (4 to 5 score). The remaining four genotypes, SP 33316, SP 33349, SP 33487 and GM 15018, had light coloured glumes (2 to 3 score).

Seed colour (SD-CL): Most of the genotypes, except IS 14387, IS 18528, SP 33349, IS 14375 and SP 33487, were found white seeded.

Glume index (GL-INDX): Among genotypes, the glume index varied from 1.1 to 2.6 exhibiting a wide range of length / breadth ratio.

4.1.2 Correlations

Correlations between different characters: Correlation coefficients estimated between 17 characters recorded on 22 genotypes are given in Table 5. Field grade score (FGS) showed strong positive correlations with threshed grade score (r =

Table 5. Correlations between different variables in 22 sorghum genotypes

1. FGS	1.000																	
2. TGS	0.929*	1.000																
3. %GER	-0.843 *	-0.905*	1.000															
4. ERGO	0.777*	0.742*	-0.826*	1.000														
5. G-PHEN	-0.167	0.037	-0.037	-0.272	1.000													
6. G-PHEN*	-0.513*	-0.403	0.311	-0.402	0.758*	1.000												
7. S-PHEN	-0.597*	-0.608*	0.485*	-0.420*	0.261	0.642*	1.000											
8. S-PHEN*	-0.682*	-0.602*	0.518*	-0.536*	0.349	0.722*	0.774*	1.000										
9. G-FLAV	-0.446*	-0.491*	0.422*	-0.369	0.301	0.505*	0.396	0.516*	1.000									
10. S-FLAV	-0.403	-0.428*	0.385	-0.335	0.269	0.453*	0.408	0.554*	0.918*	1.000								
11. S-HRD	-0.786*	-0.828*	0.861*	-0.806*	-0.041	0.259	0.295	0.483*	0.313	0.304	1.000							
12. DF	0.141	0.251	-0.225	0.366	-0.215	-0.304	-0.243	-0.168	-0.262	-0.256	-0.169	1.000						
13. HT	-0.597*	-0.638*	0.700*	-0.482*	-0.422*	-0.136	0.175	0.225	0.089	0.081	0.674*	0.375	1.000					
14. YD/PL	0.498*	0.625*	-0.509*	0.532*	0.014	-0.184	-0.461*	-0.338	-0.497*	-0.467*	-0.469*	0.624*	-0.123	1.000				
15. G-COV	-0.495*	-0.504*	0.560*	-0.364	0.036	0.154	0.530*	0.448*	0.360	0.433*	0.279	0.028	0.451*	-0.394*	1.000			
16. GLCL	-0.753*	-0.729*	0.612*	-0.559*	0.243	0.612*	0.655*	0.685*	0.573*	0.521*	0.616*	-0.121	0.351*	-0.437*	0.333	1.000		
17. SDCL	-0.659*	-0.528*	0.423*	-0.444*	0.425*	0.704*	0.683*	0.921*	0.548*	0.629*	0.387	-0.225	0.066	-0.355	0.447*	0.615*	1.000	
18. GL-IN	-0.188	-0.290	0.256	-0.166	0.041	0.334	0.551*	0.460*	0.245	0.278	0.228	-0.194	0.024	-0.254	0.203	0.245	0.356	1.000
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18

* Significant at p = 0.05

0.93) and ergosterol content (r = 0.78), and strong negative correlations with germination percentage (r = - 0.84), seed hardness (r = - 0.79), glume colour (r = - 0.75), and seed colour (r = - 0.66). Field grade score also showed significant negative correlations with acid-methanol extract of glume phenols (r = - 0.51), seed phenols (r = -0.59), flavan-4-ols in glumes (r = -0.45), and percentage glume cover (r = -0.50). Also, FGS showed significant positive correlation (r = 0.50) with grain yield plant^{-1}.

Similarly, threshed grade score (TGS) showed strong positive correlations with ergosterol content (r = 0.74) and grain yield (r = 0.63). In contrast, TGS showed strong negative correlations with seed hardness (r = -0.83), glume colour (r = -0.73), and seed phenols (r = -0.60 and -0.61). It also showed significant negative correlations with seed colour, glume coverage and glume flavan-4-ols.

Percentage seed germination revealed strong positive correlations with seed hardness (r = 0.86), glume colour (r = 0.61), plant height (r = 0.70), and seed phenols (r = 0.49 and 0.52). Like FGS and TGS, ergosterol content also revealed strong negative correlations with seed hardness (r = -0.81), glume colour (r = -0.56) and seed phenols (r = -0.54).

Glume and seed phenol contents, in general, showed high positive correlations with glume colour and seed colour. The content of glume flavan-4-ols showed moderate

positive correlations with seed and glume colours. Seed hardness showed significant positive correlations with plant height (r = 0.67) and glume colour (r = 0.62).

Intragroup correlations: The 22 genotypes were grouped based on characteristics such as seed colour, glume colour, and seed hardness (Table 6). The correlations of FGS and TGS with other characters were computed within different groups, and the estimates of intragroup correlations are given in Tables 7 and 8.

In the coloured seed group, both FGS and TGS showed strong negative correlations with glume phenols and glume colour. Likewise in the white seed group, both FGS and TGS showed significant negative correlations with grain hardness. Also in lines with straw glumes, both field grade score and threshed grade score showed strong negative correlation (r = -0.78 and r = -0.87) with seed hardness. In the coloured glume lines, TGS showed significant negative correlations with seed hardness and glume colour. In the soft seed lines, FGS and TGS exhibited high negative correlations with glume colour. In the hard seed lines, FGS and TGS showed significant negative correlations with seed phenols and seed hardness.

Correlations in the F_2 generation: Estimation of correlations in the cross between straw glume (S_2) × purple glume (R_1) revealed (Table 9) that FGS and TGS show

Table 6. Grouping of sorghum genotypes based on morphological characters.

Genotype	Seed colour	Glume colour	Seed hardness
AKMS 14B	-	-	-
296B	-	-	-
AKR 150	-	-	-
MS 422B	-	+	-
R 1413	-	-	-
IS 14375	+	+	+
IS 14387	+	+	+
IS 18144	+	+	-
IS 18528	+	+	+
IS 24495	-	-	+
IS 25017	-	+	+
SP 33316	-	+	-
SP 33349	+	+	+
SP 33487	+	+	-
GM 15018	-	+	-
GM 15373	-	+	+
TNS 30	-	-	-
B58586	-	-	+
GMRP 13	-	-	-
IS 21443	-	-	+
SPV 462	-	-	-
SPV 475	-	-	-

Seed colour + = coloured seed, Glume colour + = coloured glume, Seed hardness + = hard seed
Seed colour - = white seed, Glume colour - = straw glume, Seed hardness - = soft seed.

Table 7. Correlation matrix in different sorghum lines for Field Grade Score.

Char	22 Lines	Lines with coloured seed	Lines with white seed	Lines with straw glume	Lines with coloured glume	Lines with hard seed	Lines with soft seed
FGS	1.000	1.000	1.000	1.000	1.000	1.000	1.000
TGS	0.929*	0.846*	0.939*	0.935*	0.860*	0.936*	0.854*
%GER	-0.843*	-0.627	-0.835*	-0.827*	-0.726*	-0.738*	-0.748*
ERGO	0.777*	0.547	0.753*	0.729*	0.664*	0.512	0.721*
G-PHEN	-0.167	0.941*	0.004	0.315	0.449	0.084	-0.706*
G-PHEN*	-0.513*	0.173	0.223	0.315	-0.450	-0.532	-0.827*
S-PHEN	-0.597*	-0.310	-0.039	0.097	-0.607	-0.693	-0.667*
S-PHEN*	-0.682*	-0.566	0.039	0.004	-0.755*	-0.779*	-0.641*
G-FLAV	-0.446*	0.208	-0.217	0.000	-0.172	-0.195	-0.518
S-FLAV	-0.403	0.319	0.000	0.000	-0.211	-0.127	-0.595*
S-HRD	-0.786*	-0.605	-0.807*	-0.783*	-0.582	-0.757*	-0.521
DF	0.141	-0.654	0.090	0.126	-0.350	-0.288	-0.308
HT	-0.597*	-0.891*	-0.671*	-0.818*	-0.690*	-0.342	-0.255
YD/PL	0.498*	0.073	0.366	0.542	0.249	-0.142	0.377
G-COV	-0.495*	0.008	-0.301	-0.494	-0.604	0.075	-0.498
GL-CL	-0.753*	-0.761	-0.458	0.000	-0.600	-0.683	-0.766*
SD-CL	-0.659	0.032	0.000	0.000	-0.609	-0.640	-0.634*
GL-INDX	-0.188	-0.349	0.170	0.076	-0.635*	-0.403	-0.028

* Significant at p = 0.05

FGS= Field grade score, TGS= Threshed grade score, %GER= Germination, ERGO= Ergosterol, G-PHEN= Glume phenol, G-PHEN*= Glume phenol in acid methanol, S-PHEN= Seed phenol, S-PHEN*= Seed phenol in acid methanol, G-FLAV= Glume flavan-4-ols, S-FLAV= Seed flavan-4-ols, S-HRD= Seed hardness, DF= days to flower, HT= Plant height, YD/PL= Yield/plant, %G-COV= Glume cover, GLCL= Glume colour, SDCL= Seed colour, GLINDX= Glume index

Table 8. Correlation matrix in different sorghum lines for Threshed Grade Score.

Char	22 Lines	Lines with coloured seed	Lines with white seed	Lines with straw glume	Lines with coloured glume	Lines with hard seed	Lines with soft seed
TGS	1.000	1.000	1.000	1.000	1.000	1.000	1.000
%GER	-0.905*	-0.935*	-0.908*	-0.915*	-0.848*	-0.706*	-0.871*
ERGO	0.743*	0.870*	0.755*	0.748*	0.674*	0.573	0.653*
G-PHEN	0.037	0.935*	0.117	0.439	0.629	0.262	-0.431
G-PHEN*	-0.404	0.036	0.111	0.428	-0.367	-0.432	-0.704*
S-PHEN	-0.608*	-0.488	0.009	-0.083	-0.608	-0.701	-0.739*
S-PHEN*	-0.602*	-0.446	0.050	0.014	-0.561	-0.767*	-0.457
G-FLAV	-0.490*	-0.151	0.280	0.000	-0.348	-0.149	-0.718*
S-FLAV	-0.428*	-0.070	0.000	0.000	-0.310	-0.090	-0.763*
S-HRD	-0.828*	-0.663	-0.850*	-0.871*	-0.640*	-0.610	-0.621*
DF	0.251	-0.252	0.282	0.361	-0.163	-0.092	0.463
HT	-0.637*	-0.918*	-0.603*	-0.730*	-0.732*	-0.300	-0.306
YD/PL	0.625*	0.559*	0.514*	0.710*	0.440*	0.114	0.543
G-COV	-0.509*	-0.300	-0.333	-0.514	-0.521	-0.055	-0.443
GL-CL	-0.729*	-0.974*	-0.345	0.000	-0.727*	-0.494	-0.840*
SD-CL	-0.528*	0.200	0.000	0.000	-0.339	-0.627	-0.308
GL-INDX	-0.290	-0.588	0.080	-0.001	-0.702*	-0.478	-0.186

*Significant at p = 0.05

TGS=Threshed grade score, %GER=Germination, ERGO=Ergosterol, G=PHEN=Glume phenol, G-PHEN*= Glume phenol in acid methanol, S-PHEN=Seed phenol, S-PHEN*=Seed phenol in acid methanol, G-FLAV=Glume flavan-4-ols, S-FLAV=Seed flavan-4-ols, S-HRD=Seed hardness, DF=days to flower, HT=Plant height, YD/PL=Yield/plant, %G-COV=Glume cover, GLCL=Glume colour, SDCL=Seed colour, GLINDX=Glume index.

Table 9. Correlation matrix in F_2 of a cross $S_5 \times R_1$ in sorghum.

1 FGS	1.0000					
2 TGS	0.8748*	1.0000				
3 G-COV	-0.0670	-0.1391	1.0000			
4 SD-CL	-0.1778	-0.2942	0.0933	1.0000		
5 DF	-0.0307	-0.0136	0.0135	0.0422	1.0000	
6 GL-CL	-0.3998*	-0.4917*	-0.0212	0.1590	0.0955	1.0000
	1	2	3	4	5	6

* Significant at p = 0.05

1. FGS = Field Grade Score, 2. TGS = Threshed Grade Score, 3. %G-COV Percentage glume cover, 4. SDCL = Seed colour, 5. DF = Days to flower, 6. GLCL= Glume colour.

high negative correlations with glume colour (r = -0.40 and -0.49, respectively) and low negative correlations with seed colour (r = -0.18 and -0.29, respectively).

Also, Figs 2 and 3 illustrate the relations of field grade score and threshed grade score with glume colour in different families of the cross straw glume (S_5) × coloured glume (R_1). In P_2, BC_2 and F_1 families, the FGS and TGS values decreased as the intensity of glume colour increased. Obviously, both FGS and TGS are negatively associated with glume colour.

4.2 GENERATION MEAN ANALYSIS FOR GRAIN MOULDS IN DIFFERENT CROSSES OF SORGHUM

Sorghum genotypes utilised in the crossing programme and their ancillary data are given in Table 3 and Plate 6.

4.2.1 Field grade score (FGS)

Family means: Mean values for field grade score of the parents, F_1, F_2, and backcross generations raised during 1995 *kharif*, are given in Table 10. The mean values for FGS of susceptible lines S_1, S_5 and S_6, were consistently high over the years. They ranged from 4.6 to 4.9, on a scale of 1 to 5 where 1 = no moulds and 5 = more than 50% moulds, during 1994 (Table 4) and were consistently high during

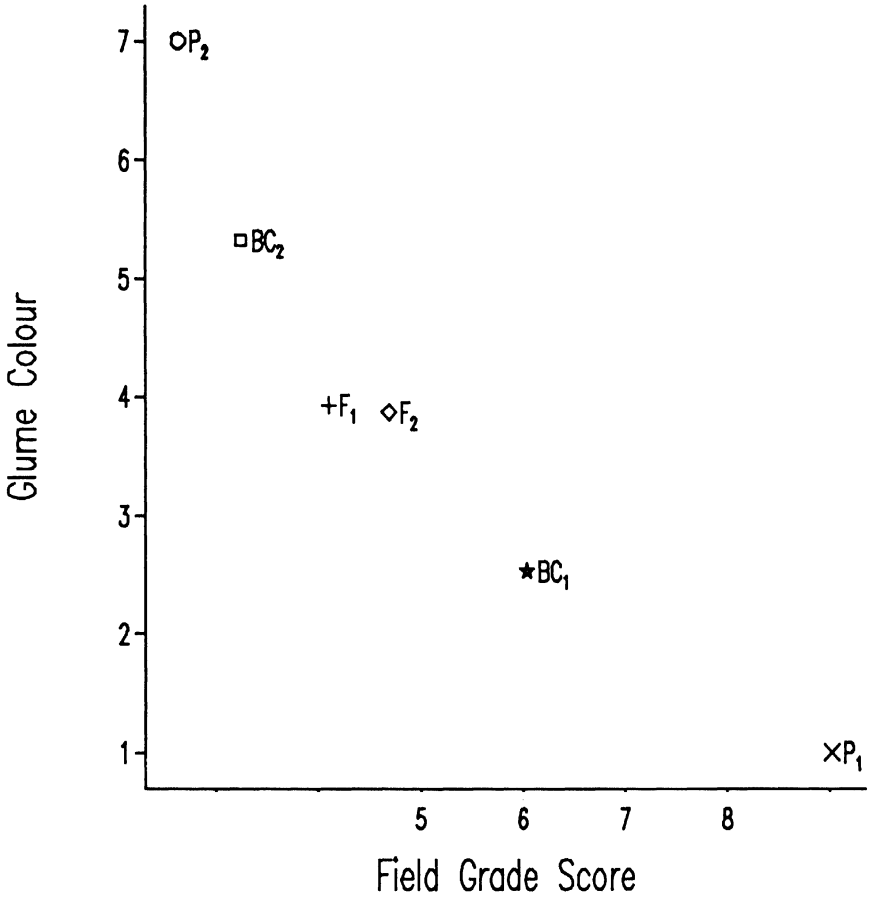


Figure 2. The relation of field grade score with glume colour in different families of the cross S_5 (P_1) x R_1 (P_2).

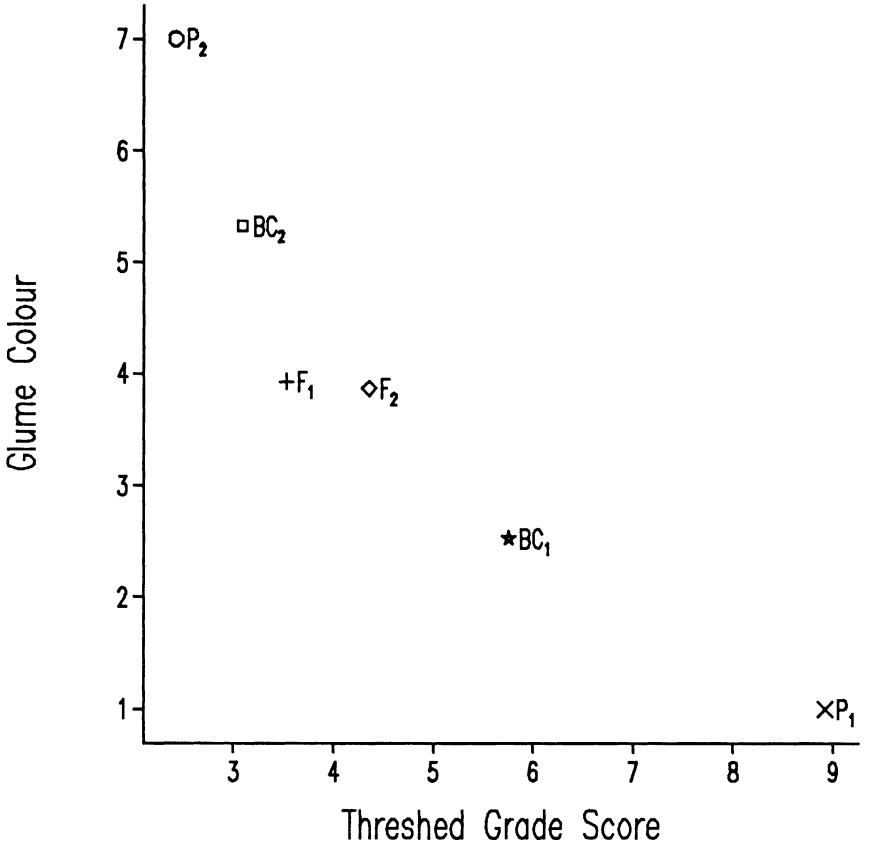


Figure 3. The relation of threshed grade score with glume colour in different families of the cross S_5 (P_1) x R_1 (P_2).

Plate 6. A - Grain mould susceptible sources utilised in crossing programme; AKMS 14B, MS 422B and AKR 150.
B - Grain mould resistant sources utilised in crossing programme, IS 14375, IS 14387 and IS 25017.

Plate 6

B

Table 10. Means of the six families for field grade score in different crosses of sorghum during 1995.

Families		$S_1 \times R_1$	$S_2 \times R_1$	$S_5 \times R_1$	$S_6 \times R_1$	$S_1 \times R_2$	$S_2 \times R_2$	$S_3 \times R_2$	$S_1 \times R_3$	$R_2 \times R_3$	$R_1 \times R_2$
										2.70	
P_1	M	8.67	7.37	9.03	8.47	8.33	8.50	8.13	8.96	~~9.27~~	2.50
	SE	0.12	0.19	0.06	0.13	0.11	0.09	0.20	0.33	0.21	0.11
P_2	M	2.57	2.20	2.63	2.40	2.87	2.60	2.73	8.20	7.63	2.50
	SE	0.10	0.09	0.16	0.10	0.16	0.12	0.11	0.16	0.21	0.16
F_1	M	3.00	2.90	4.10	3.40	3.70	3.63	4.03	8.60	3.43	2.73
	SE	0.10	0.15	0.38	0.22	0.14	0.15	0.21	0.09	0.16	0.21
BC_1	M	6.16	5.22	6.04	6.71	6.80	5.18	6.64	8.78	3.42	3.13
	SE	0.29	0.30	0.30	0.27	0.31	0.31	0.27	0.08	0.13	0.22
BC_2	M	3.69	2.89	3.24	2.78	3.02	3.64	4.04	8.29	5.82	2.73
	SE	0.26	0.20	0.19	0.14	0.13	0.15	0.20	0.12	0.33	0.10
F_2	M	4.60	3.63	4.69	4.78	4.72	4.37	6.04	8.43	5.53	3.21
	SE	0.12	0.11	0.13	0.13	0.14	0.12	0.14	0.05	0.14	0.08

M = Mean, SE = Standard error.

1995 and 1996 (8.30 to 9.00 and 8.63 to 8.97, respectively), on a scale of 1 to 9 where 1= no moulds and 9 = 75% moulded (Tables 10 and 11). The lines S_2 and S_3 showed moderate resistance during 1994 (scores 3.1 to 3.3 on a scale of 1 to 5) but showed high mean value during 1995 (7.37 to 8.50 on a 1 to 9 scale). Two resistant lines, R_1 and R_2 consistently showed low mean values for FGS over the years. Field grade scores varied from 1.4 to 1.6 (scale of 1 to 5) during 1994, 2.20 to 2.87 during 1995, and 2.97 to 3.93 during 1996, (scale of 1 to 9 was used during 1995 and 1996). The white resistant source, R_3, recorded a mean value of 2.83 on a scale of 1 to 5 during 1994, but became susceptible during 1995 (mean values varied from 7.63 to 8.20). However R_3 showed low resistance with mean FGS values ranging from 6.23 to 6.40 during 1996.

In seven out of ten crosses evaluated during 1995, the F_1 means were significantly different from that of P_1 (susceptible parent) and P_2 (resistant parent), but they tended towards the resistant parents. The F_2 means were significantly different from those of the other five generations and tended towards the resistant parents. The means of BC_1, in general, tended towards the P_1, whereas the means of BC_2 were greater than that of P_2 but less than that of BC_1 and P_1.

The remaining three crosses, $R_1 \times R_2$, $S_1 \times R_3$ and $R_2 \times R_3$, showed different patterns. In $R_1 \times R_2$, the mean values of P_1 and P_2 were not significantly different and there was little variation in the means of F_1, F_2, BC_1, and BC_2. In $S_1 \times R_3$, the mean values of P_1

and P_2 were significantly different; the mean value of F_1 was equal to the mid-parent value, and the BC_2 mean was equal to that of P_2. In $R_2 \times R_3$, the mean value of P_1 was less than that of P_2, while mean values of F_1 and BC_1 were similar to that of P_1 parent. However, the F_2 mean was significantly different from those of all other generations, while the mean values of BC_2 and F_2 tended towards P_2.

The list of crosses tested during 1996 is shown in Table 3. The family means of different crosses, grown during 1996, for field grade score, are given in the Table 11. In four crosses, $S_1 \times R_1$, $S_1 \times R_2$, $S_1 \times R_3$, and $S_5 \times R_1$ the F_1 means were significantly different from the mid-parent value and tended towards the more resistant parent. In the cross, $S_1 \times R_1$, the mean values of BC_1 and BC_2 were not significantly different. In two crosses, $S_1 \times R_6$ and $S_1 \times R_{16}$, the F_1 means were less than those of both the parents. Also, the mean values of BC_1 and BC_2 were less than those of recurrent parents. In $S_1 \times R_6$, the F_2 was similar to that of BC_2. Whereas in $S_1 \times R_{16}$, the F_2 mean was similar to that of BC_1; in this cross, the mean values of F_1, BC_1, BC_2, F_2 were greater than those of both the parents. In $R_2 \times R_3$, the mean values of F_1, F_2, BC_1, and BC_2 tended towards the R_3, the more susceptible of the two parents.

Frequency distributions: Frequency distributions for field grade score (FGS) of P_1, P_2, F_1, BC_1, BC_2, and F_2 families of ten crosses grown during 1995 are depicted in Figs 4 to 6. In five crosses, $S_1 \times R_1$, $S_1 \times R_2$, $S_3 \times R_2$, $R_2 \times R_3$, and $S_6 \times R_1$ (Figs 5 and 6), the F_2 distributions showed bimodal pattern. The F_1 distributions, in general, were

Table 11. Means of the families for field grade score in different crosses of sorghum during 1996.

Families		$S_1 \times R_1$	$S_1 \times R_2$	$S_1 \times R_3$	$S_1 \times R_6$	$S_1 \times R_{16}$	$S_5 \times R_2$	$R_1 \times R_2$	$R_2 \times R_3$
P_1	M	8.63	8.73	8.77	8.93	8.97	8.77	2.97	2.97
	SE	0.14	0.11	0.09	0.04	0.03	0.20	0.14	0.12
P_2	M	3.57	3.93	6.23	8.50	7.87	3.73	2.77	6.40
	SE	0.11	0.21	0.13	0.13	0.15	0.18	0.13	0.11
F_1	M	4.13	4.70	6.33	8.23	7.07	5.00	4.53	5.03
	SE	0.12	0.15	0.14	0.16	0.20	0.16	0.24	0.16
BC_1	M	4.53	5.09	6.04	8.67	7.89	5.59	4.67	5.78
	SE	0.13	0.15	0.18	0.11	0.16	0.14	0.24	0.16
BC_2	M	4.40	4.58	5.80	8.31	7.45	4.58	4.51	6.04
	SE	0.13	0.11	0.13	0.15	0.15	0.11	0.17	0.08
F_2	M	4.75	4.72	5.96	8.32	8.01	4.99	5.12	5.97
	SE	0.09	0.06	0.07	0.06	0.08	0.07	0.09	0.08

M = Mean, SE = Standard error.

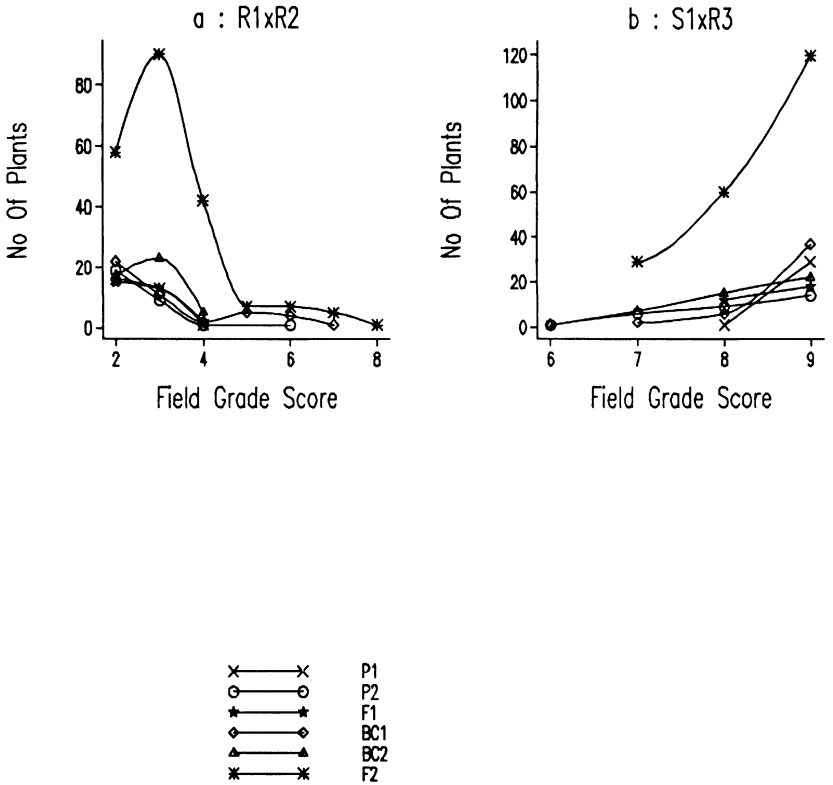


Figure 4. Frequency distributions of P_1, P_2, F_1, F_2, BC_1 and BC_2 families in different crosses of sorghum for FGS (1995).

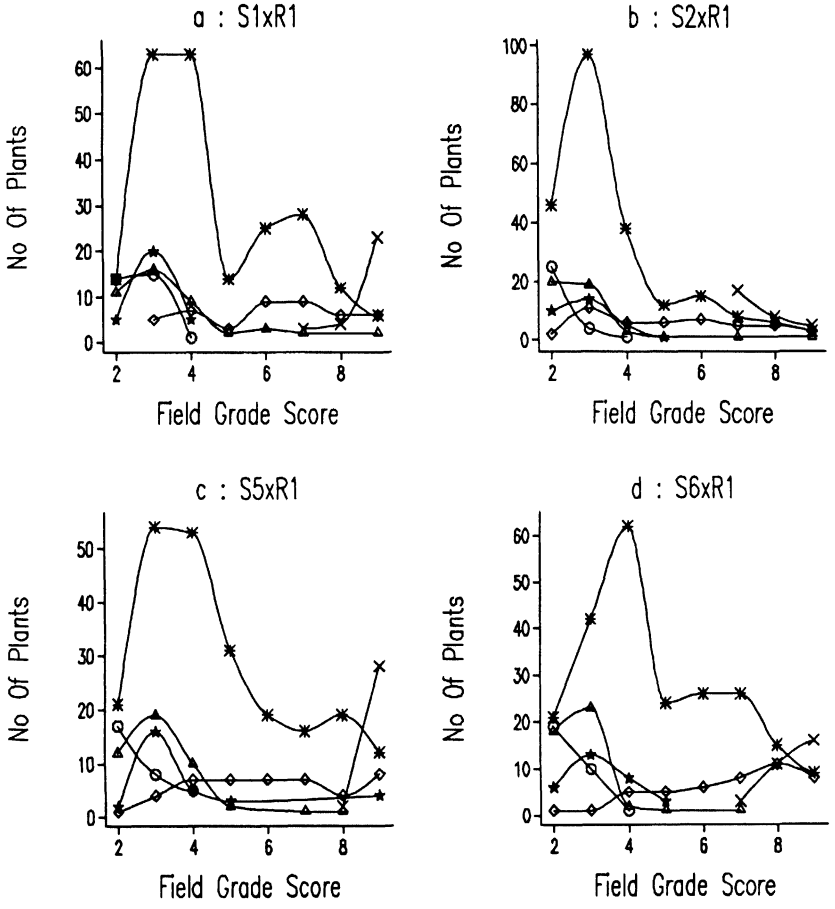


Figure 5. Frequency distributions of P_1, P_2, F_1, F_2, BC_1 and BC_2 families in different crosses of sorghum for FGS (1995).

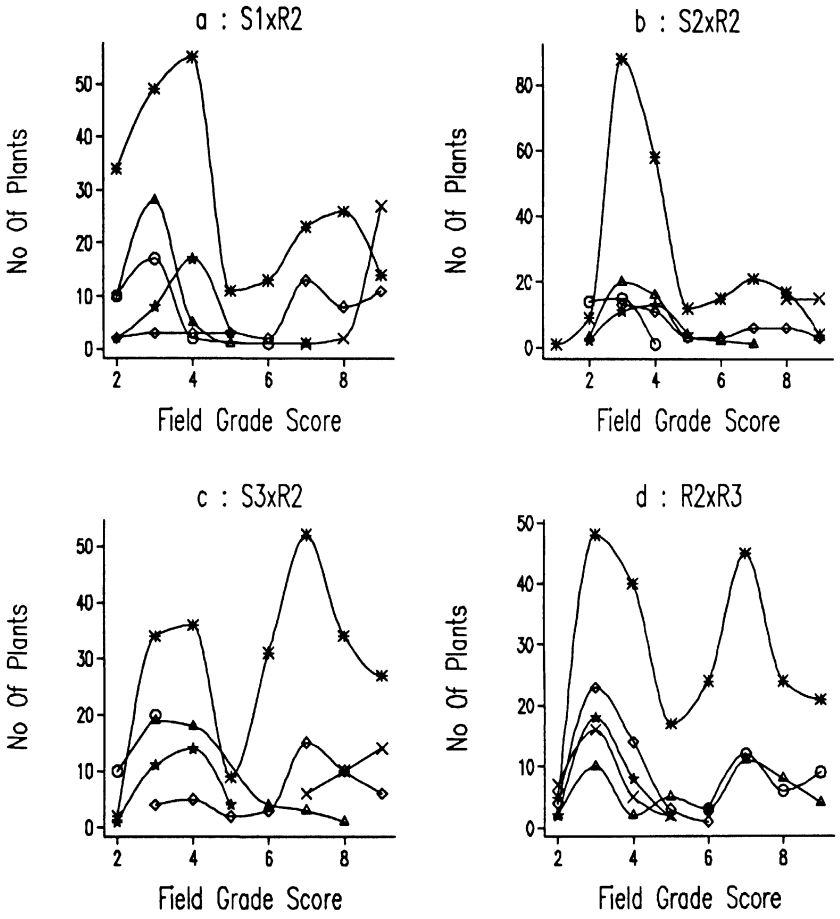


Figure 6. Frequency distributions of P_1, P_2, F_1, F_2, BC_1 and BC_2 families in different crosses of sorghum for FGS (1995).

skewed towards the resistant parents (P_2). The distributions in BC_2 were somewhat similar to that of F_2. Also the distributions of BC_1 and BC_2 tended to overlap.

In the white susceptible (S_1) × white resistant (R_3) cross, the F_1 and F_2 distributions were skewed towards the susceptible P_1 parent (Fig. 5). Further the distribution in BC_1 was similar to that of F_2. In the red resistant (R_1) × brown resistant (R_2) cross, the F_2 distribution was unimodal (Fig. 5). In this cross the distribution of BC_2 was similar to that of P_2, and an overlapping of BC_1 and BC_2 was observed.

The F_2 distributions in four crosses, $S_2 \times R_1$, $S_5 \times R_1$ $S_6 \times R_1$ and $S_2 \times R_2$, were more or less bimodal with modes in the range of 2 to 4 (Figs 5 and 6). The distributions showed an extended tail towards higher (more susceptible) scores, with small peaks forming a second mode in the range of 6 to 8. The F_1 and F_2 distributions were skewed towards the resistant parent.

Figures 7 and 8 depict the frequency distributions of different families, for field grade score, in different crosses of sorghum evaluated during 1996. The F_2 distributions were found unimodal in the crosses, $S_1 \times R_1$, $S_1 \times R_3$, $S_5 \times R_1$ and $R_2 \times R_3$, bimodal in one cross, $R_1 \times R_2$, and exponential in three crosses of $S_1 \times R_2$, $S_1 \times R_6$ and $S_1 \times R_{16}$. The F_1 distributions were skewed towards the parent with the greater resistance, and the distribution of BC_1 overlapped with that of BC_2.

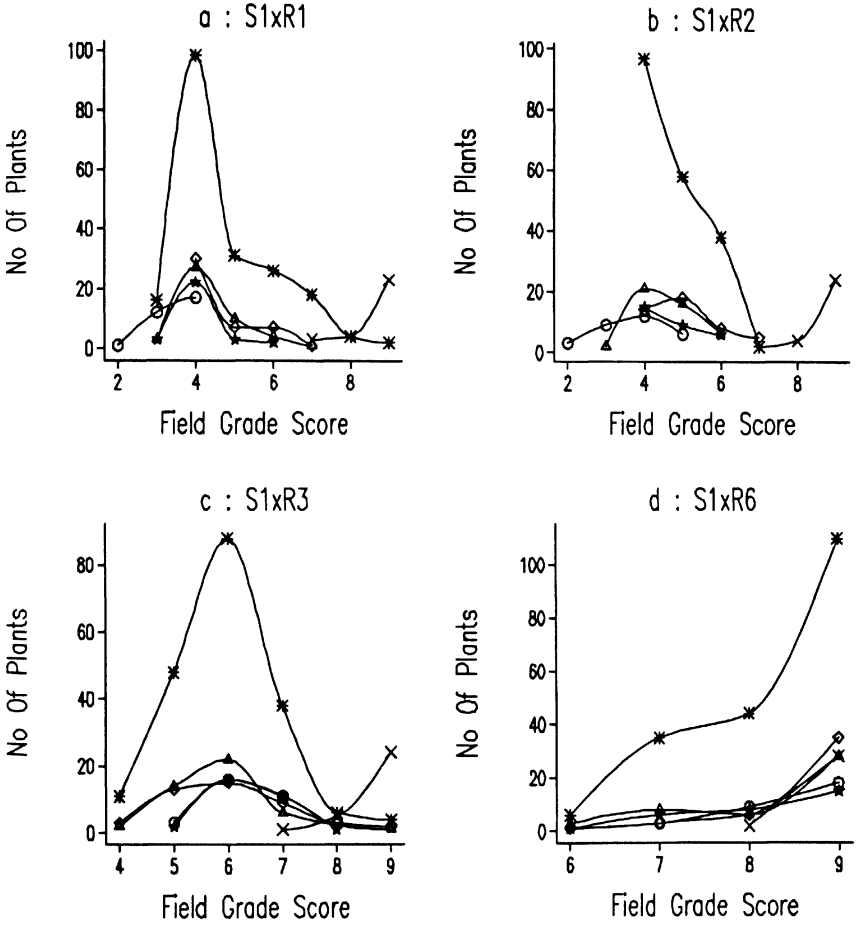


Figure 7. Frequency distributions of P_1, P_2, F_1, F_2, BC_1 and BC_2 families in different crosses of sorghum for FGS (1996).

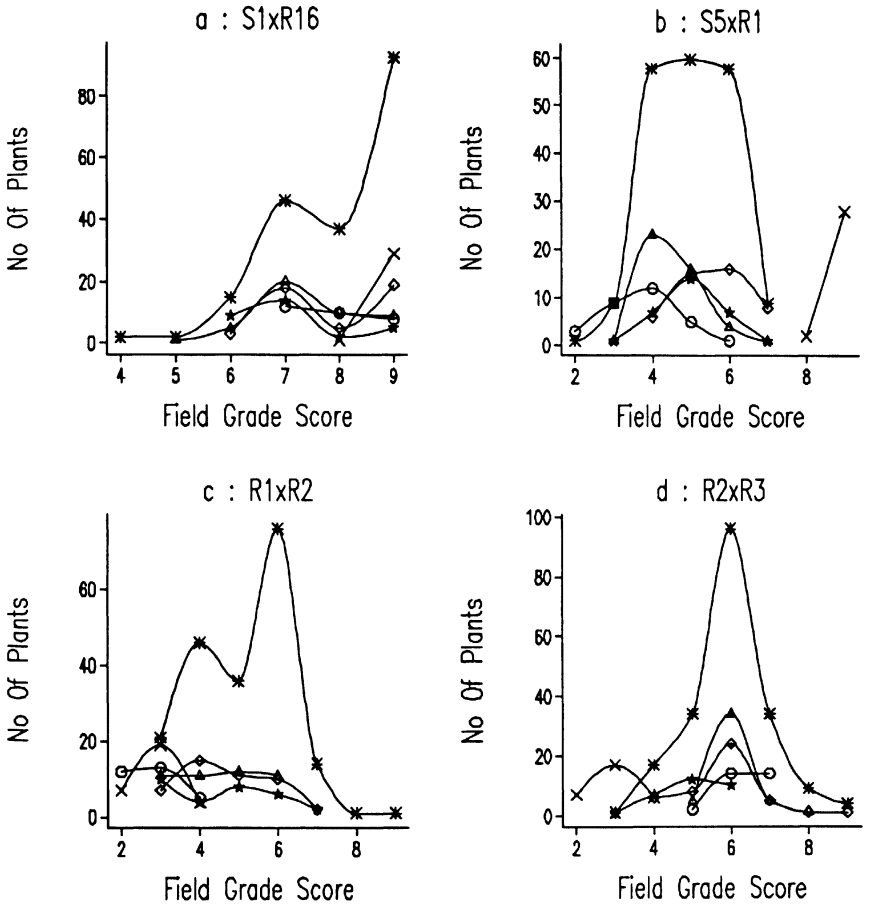


Figure 8. Frequency distributions of P_1, P_2, F_1, F_2, BC_1 and BC_2 families in different crosses of sorghum for FGS (1996).

Segregation pattern: Estimates of gene number and mode of inheritance were determined from the analysis of segregation patterns of F_2 and BC_1 populations, and the results are summarised in the Tables 12 and 17. In different crosses, segregation ratios in F_2 and BC_1, for FGS and TGS, were almost similar. The segregation patterns in F_2 and BC_1, for field grade score in various crosses between susceptible × resistant lines, are described below.

(i) White susceptible × red resistant (R_1) crosses: In three crosses, $S_1 \times R_1$, $S_5 \times R_1$ and $S_6 \times R_1$ the observed F_2 segregation pattern showed good fit to the 9 resistant (R):7 susceptible (S) ratio. The BC_1 populations segregated into 1R:3S ratio. These results may be explained by a model of two major nonallelic genes with duplicate recessive epistasis (Plate 7).

In $S_2 \times R_1$, the F_2 population segregated into 181 resistant : 44 susceptible plants which showed good fit to 53:11 ratio. Further, the segregation of BC_1 population conformed to the 1R:1S ratio (Tables 12 and 17). The F_2 segregation indicates the involvement of three major nonallelic genes.

(ii) White susceptible × brown resistant (R_2) crosses: In $S_1 \times R_2$, the F_2 segregation fitted to the modified trigenic ratio of 39R:25S, suggesting interaction among three independently assorting gene pairs (Table 12 and Plate 7).

Table 12. Segregation ratios for field grade score of F_2 and backcross populations derived from crosses of susceptible x resistant genotypes.

Cross	Generation	Resistant genotype(R)	Susceptible genotype(S)	Ratio	χ^2	Probability
$S_1 \times R_1$	F_2	140	85	9:7	3.23	0.10-0.05
	BC_1	12	33	1:3	0.07	0.80-0.70
$S_5 \times R_1$	F_2	128	97	9:7	0.04	0.90-0.80
	BC_1	12	33	1:3	0.07	0.60-0.70
$S_6 \times R_1$	F_2	125	100	9:7	0.05	0.90-0.80
	BC_1	7	38	1:3	2.13	0.20-0.10
$S_2 \times R_1$	F_2	181	44	51:13	0.08	0.80-0.70
	BC_1	19	26	1:1	1.08	0.30-0.20
$S_1 \times R_2$	F_2	137	87	39:25	0.02	0.90-0.80
	BC_1	8	37	1:3	1.24	0.30-0.20
$S_2 \times R_2$	F_2	156	69	45:19	0.10	0.80-0.70
	BC_1	24	21	1:1	0.20	0.70-0.80
$S_3 \times R_2$	F_2	82	143	27:37	3.08	0.10-0.05
	BC_1	9	36	1:7	3.35	0.10-0.05
$R_2 \times R_3$	F_2	93	132	27:37	0.02	0.90-0.80
	BC_2	8	37	1:7	1.18	0.80-0.70
$R_1 \times R_2$	F_2	190	20	57:7	0.44	0.70-0.50
	BC_1	35	10	3:1	0.19	0.70-0.50

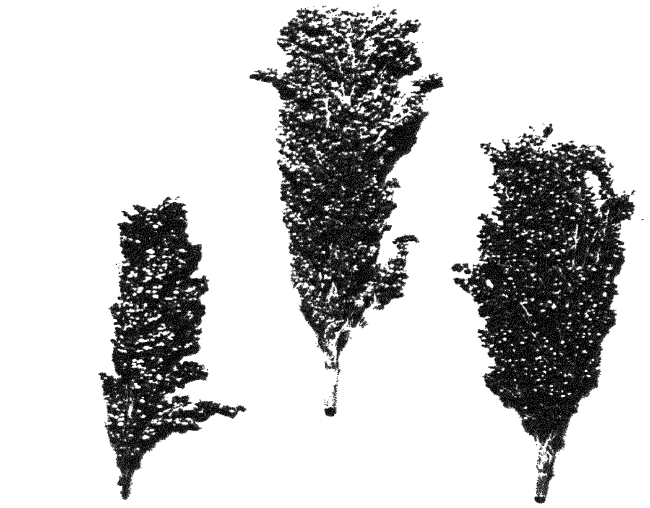
R = Resistant, S = Susceptible.

Plate 7. Parents and F_1 of white susceptible × coloured resistant crosses.

A. White susceptible (AKMS 14B, resistant F_1 and coloured resistant (IS 14375).

B. White susceptible (MS 423B), coloured resistant F_1 and coloured resistant (IS 14387).

Plate 7

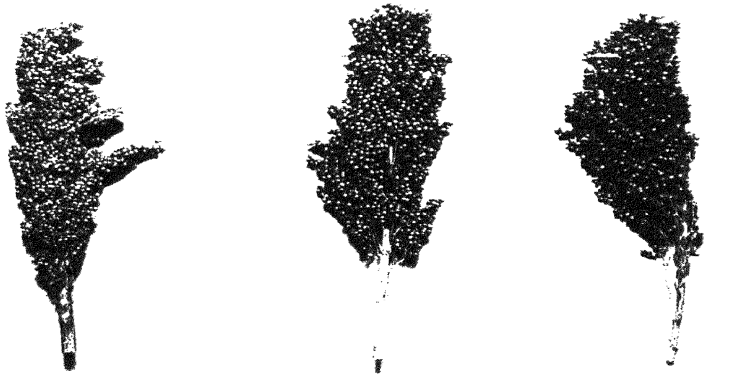


AKMS 14 B

AKMS 14 B
x
IS 14375

IS 14375

A



MS 422 B

MS 422 B
x
IS 14387

IS 14387

B

In $S_2 \times R_2$, the F_2 progeny segregated into 156 resistant : 69 susceptible plants which fitted to the 45R:19S ratio, indicating interaction among three major nonallelic genes. Also, the segregation pattern in the BC_1 fitted to the 1R:1S ratio (Table 12).

The F_2 population of $S_3 \times R_2$, segregated into 82 resistant : 143 susceptible plants which conformed to the modified trigenic ratio of 27:37, indicating interaction among three nonallelic gene pairs (Table 12). Further, the segregation pattern of BC_1 population fitted to the1R:7S ratio.

(iii) Brown resistant (R_2) × white resistant (R_3) cross: In the F_2 population of this cross, 93 resistant : 132 susceptible plants were scored (Table 12). This segregation pattern fits to the modified trigenic ratio of 27:37, suggesting complementary interaction among three nonallelic genes. The segregation pattern in the BC_2 conformed to the 1R:7S ratio.

Red resistant (R_1) × brown resistant (R_2) cross: In this cross, the F_2 population segregated into 190 resistant : 20 susceptible plants, which showed good fit to the trigenic ratio of 57:7 (Table 12). This modified ratio indicates complex interaction among three major genes; the segregation pattern in the BC_1 population fitted to the 3R:1S ratio.

Generation mean analysis: Estimates of genetic effects for field grade score, recorded during 1995, are given in the Table 13. The R^2 values obtained in ten crosses were very high (84 to 100%), indicating that the model was a good fit. Estimates of additive gene effects [d] were found significant in all the ten crosses. In five of the crosses, $S_2 \times R_1$, $S_5 \times R_1$, $S_1 \times R_2$, $S_2 \times R_2$ and $R_1 \times R_2$, significant negative dominance gene effects [h] were observed. In these crosses, the estimates of additive gene effects were greater than the estimates of dominance gene effects. In general, dominance × dominance gene interactions [l] were found exclusively in the crosses where dominance effects were absent. In three crosses, $S_6 \times R_1$, $S_1 \times R_2$, $S_2 \times R_2$, significant additive × dominance interactions [j] were observed.

Estimates of genetic effects for field grade score in different crosses grown during 1996 are given in the Table 14. Significant additive gene effects were observed in all crosses except $R_1 \times R_2$. In contrast, significant negative dominance gene effects were observed in only two of the eight crosses studied. Among interaction effects, additive × additive interaction was found most frequent in all but one cross. However, in five crosses additive × dominance gene effects were greater in magnitude and were in the opposite direction.

4.2.2 Threshed grade score (TGS)

Table 13. Estimates of gene effects for field grade score in different crosses of sorghum during 1995.

Cross	S_1xR_1	S_2xR_1	S_5xR_1	S_6xR_1	S_1xR_2	S_2xR_2	S_3xR_2	S_1xR_3	R_2xR_3	R_1xR_2
[m]	5.198*	4.732*	5.829*	5.435*	5.858*	5.513*	6.558*	8.505*	5.486*	3.731*
[d]	3.027*	2.527*	3.195*	3.033*	2.980*	2.960*	2.693*	0.459*	-2.393*	
[h]		-1.877*	-2.122*	-0.643	-2.143*	-2.015*			-1.099*	
[i]	0.423*						-1.155*		-1.247*	
[j]				1.847*	1.252*	-2.621*				
[l]	-2.193*			-1.391*			-2.564*		-2.038*	
R^2	99.54	98.36	99.84	99.99	99.89	99.67	98.69	95.18	90.03	83.96

* significant at p = 0.05

Table 14. Estimates of gene effects for field grade score in sorghum during 1996.

Cross	$S_1 \times R_1$	$S_1 \times R_2$	$S_1 \times R_3$	$S_1 \times R_6$	$S_1 \times R_{16}$	$S_5 \times R_1$	$R_1 \times R_2$	$R_2 \times R_3$
[m]	6.10*	4.66*	5.94*	8.34*	9.00*	4.93*	5.34*	6.41*
[d]	2.53*	2.46*	1.29*	0.23*	0.55*	2.51*		-1.71*
[h]	-4.01*				-2.06*			
[i]		1.58*	1.51*	0.37*	-0.59*	1.24*	-2.46*	-1.68*
[j]	-4.79*	-3.70*	-1.63*			-2.90*		2.35*
[l]	2.04*						-0.78*	-1.32*
R^2	97.20	98.52	92.40	96.06	97.86	97.48	99.01	90.65

* Significant at p = 0.05

Family means: The mean value of susceptible lines S_1, S_5 and S_6 were consistently high within and over the years 1994, 1995 and 1996. Mean values of three lines ranged from 4.7 to 4.9 on a scale of 1 to 5 where 1 = no mould and 5 = > 50% mould during 1994 (Table 4). They were also consistently high during 1995 and 1996, ranging from 7.97 to 8.93 and 8.30 to 8.57, respectively, on a scale of 1 to 9 (Table 15 and 16). Two lines, S_2 and S_3 were moderately resistant during 1994 (scores 3.3 to 3.47 on a scale of 1 to 5), but showed high mean values during 1995 (7.20 to 7.83 on a scale of 1 to 9). On the other hand resistant lines R_1 and R_2 consistently showed low TGS values within and over the years. TGS values varied from 1.87 to 1.91 on a scale of 1 to 5 during 1994, and from 2.00 to 2.43 on a scale of 1 to 9 during 1995. TGS values were slightly higher (2.50 to 3.47) during 1996 compared to previous years. The white resistant source (R_3) recorded a mean value of 3.1 on a scale of 1 to 5 during 1994 but became susceptible during 1995 with TGS values ranging from 7.43 to 8.03. However, it showed a moderate mean value of 5.60 to 5.63 during 1996.

Mean values of six families in different crosses, grown during 1995, for threshed grade score are given in the Table 15. In all the crosses, except $S_1 \times R_3$, $R_1 \times R_2$ and $R_2 \times R_3$, the mean TGS values of F_1s were significantly different from those of both the parents. Also, the mean TGS values of F_1 tended towards the resistant parent. Likewise, the mean TGS value of BC_1 and BC_2 generations tended towards the

Table 15. Means of the six families for threshed grain mould score in different crosses of sorghum during 1995.

Families		$S_1 \times R_1$	$S_2 \times R_1$	$S_5 \times R_1$	$S_6 \times R_1$	$S_1 \times R_2$	$S_2 \times R_2$	$S_3 \times R_2$	$S_1 \times R_3$	$R_2 \times R_3$	$R_1 \times R_2$
P_1	M	8.03	7.20	8.93	8.10	7.97	7.67	7.83	8.50	2.67	2.03
	SE	0.16	0.12	0.05	0.14	0.19	0.13	0.17	0.12	0.15	0.03
P_2	M	2.30	2.00	2.43	2.27	2.17	2.37	2.20	8.03	7.43	2.20
	SE	0.09	0.05	0.13	0.08	0.06	0.10	0.09	0.14	0.14	0.07
F_1	M	2.87	2.23	3.53	2.80	2.73	2.73	3.23	8.17	2.83	2.50
	SE	0.14	0.07	0.42	0.18	0.08	0.12	0.14	0.15	0.18	0.19
B_1	M	5.87	4.71	5.76	5.89	6.49	4.58	6.09	8.22	2.73	2.96
	SE	0.30	0.33	0.32	0.31	0.30	0.32	0.31	0.13	0.12	0.26
B_2	M	3.44	2.49	3.09	2.78	2.42	3.11	3.27	8.00	5.53	2.60
	SE	0.24	0.15	0.18	0.15	0.09	0.17	0.22	0.13	0.34	0.12
F_2	M	4.80	3.31	4.36	4.48	4.50	3.78	5.50	8.20	5.03	2.90
	SE	0.11	0.11	0.13	0.13	0.15	0.12	0.15	0.05	0.15	0.08

M = Mean, SE = Standard error.

respective recurrent parent. The F_2 means were significantly different from those of the other five generations and these tended towards the resistant P_2 parent.

In cross $S_1 \times R_3$, even though the parental means differed significantly, the difference between them was not large. The means of BC_1, BC_2, and F_1 were similar to those of P_2 and the mean of F_2 was close to those of midparent value. Further, the difference between the means of F_1 and BC_1 was found nonsignificant, while the mean values of P_2 and F_2 were close to the mid-parent value. In the cross $R_1 \times R_2$ the difference between the parental mean values was nonsignificant, and the means of F_1, BC_1, BC_2, and F_2 were greater than those of both the parents (Table 15). However, the mean values of F_1 and BC_2 did not show significant difference.

The means of different families in eight crosses, grown during 1996, are given in Table 16. In four crosses, $S_1 \times R_1$, $S_1 \times R_2$, $S_1 \times R_3$ and $S_5 \times R_1$, the F_1 mean values were significantly different from those of both the parents, but tended towards the resistant parent. Also the F_2 means, in general, tended towards the resistant parent. Likewise, the mean values of BC_1 and BC_2 tended towards the recurrent parent. In the cross, $S_1 \times R_6$, the F_1 mean tended towards P_2 and the means of BC_1, BC_2, and F_2 were intermediate between those of parents.

In two crosses, $S_1 \times R_{16}$ and $R_1 \times R_2$, the parental mean values showed negligible differences. In $S_1 \times R_{16}$, both the parents were susceptible and the mean values of the

Table 16. Means of the families for threshed grade score in different crosses of sorghum during 1996.

Famlies		$S_1 \times R_1$	$S_1 \times R_2$	$S_1 \times R_3$	$S_1 \times R_6$	$S_1 \times R_{16}$	$S_5 \times R_1$	$R_1 \times R_2$	$R_2 \times R_3$
P_1	M	8.30	8.37	8.40	8.50	8.23	8.57	3.13	2.80
	SE	0.15	0.13	0.12	0.11	0.16	0.24	0.16	0.15
P_2	M	3.03	3.47	5.67	7.37	8.33	2.97	2.50	5.60
	SE	0.12	0.21	0.17	0.18	0.15	0.14	0.14	0.16
F_1	M	3.87	4.30	6.10	7.43	6.97	4.00	4.50	3.73
	SE	0.14	0.17	0.17	0.19	0.15	0.10	0.24	0.12
BC_1	M	4.29	4.93	6.02	8.09	7.69	4.36	4.42	4.89
	SE	0.13	0.14	0.17	0.13	0.18	0.14	0.14	0.18
BC_2	M	4.29	4.18	5.53	8.00	7.71	3.62	4.24	5.09
	SE	0.14	0.12	0.13	0.11	0.18	0.13	0.14	0.15
F_2	M	4.68	4.23	5.82	7.92	7.63	4.14	4.88	5.19
	SE	0.09	0.06	0.07	0.07	0.08	0.07	0.10	0.11

M = Mean, SE = Standard error.

F_1, BC_1, BC_2 and F_2 were less than those of both parents. Conversely, in $R_1 \times R_2$, both the parents were resistant and the TGS means of four families were greater than those of the both parents. In $R_2 \times R_3$, the F_1 mean value tended towards P_1 while the mean values of BC_1, BC_2 and F_2 tended towards P_2.

Frequency distributions: Frequency distributions of different families for TGS in eighteen crosses, grown during 1995 and 1996, are depicted in Figs 9 to 13. The F_2 generations of three crosses, $S_1 \times R_2$, $S_3 \times R_2$ and $R_2 \times R_3$, showed distinct bimodal distributions (Fig. 11). The distributions of F_1 hybrids were skewed towards the lower parent, while the distributions of BC_1 and BC_2 overlapped with those of recurrent parents. In the BC_1 of $S_1 \times R_2$, $S_3 \times R_2$, and in the BC_2 of $R_2 \times R_3$ plants were observed in all the categories from 2 to 9. On the other hand in $S_1 \times R_1$, $S_2 \times R_1$, $S_5 \times R_1$, $S_6 \times R_1$ and $S_2 \times R_2$, the F_2 frequency distributions were unimodal with one end of the curve tapering (Figs 10 and 11). The distributions of the F_1 hybrids were skewed towards the resistant parent.

In most of the crosses, the distributions of BC_1 and BC_2 overlapped with those of recurrent parent, and were found relatively even over 2 to 9 categories. In $R_1 \times R_2$ and $S_1 \times R_3$, the F_2 distribution was continuous from 6 to 9 range with a mode at 8 (Fig. 9). However the distribution of F_1 overlapped with those of both the parents.

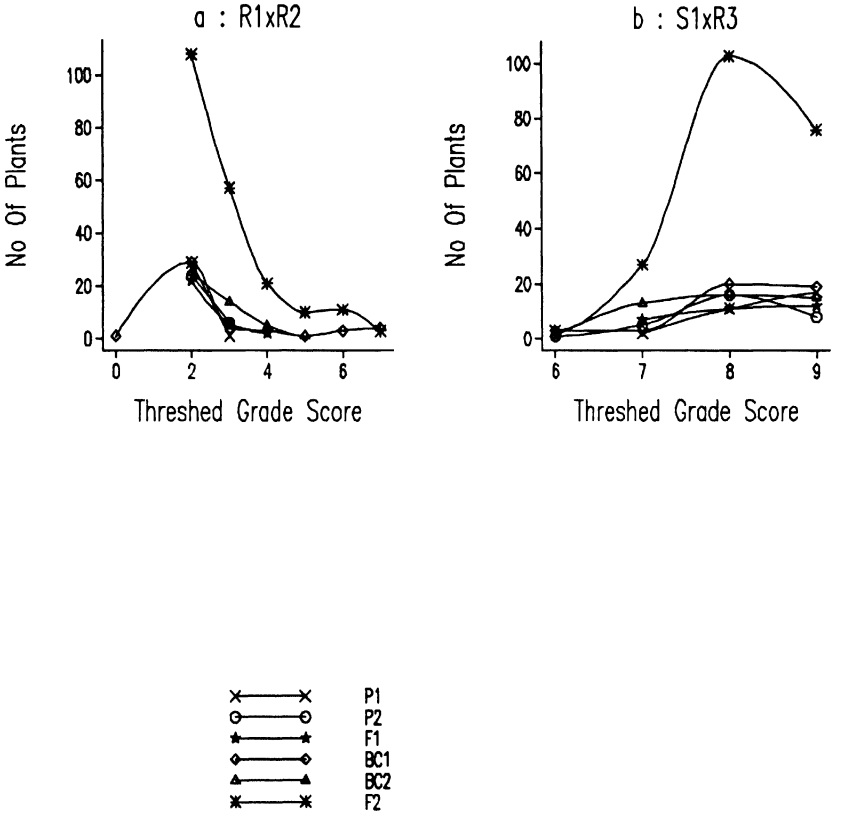


Figure 9. Frequency distributions of P_1, P_2, F_1, F_2, BC_1 and BC_2 families in different crosses of sorghum for TGS (1995).

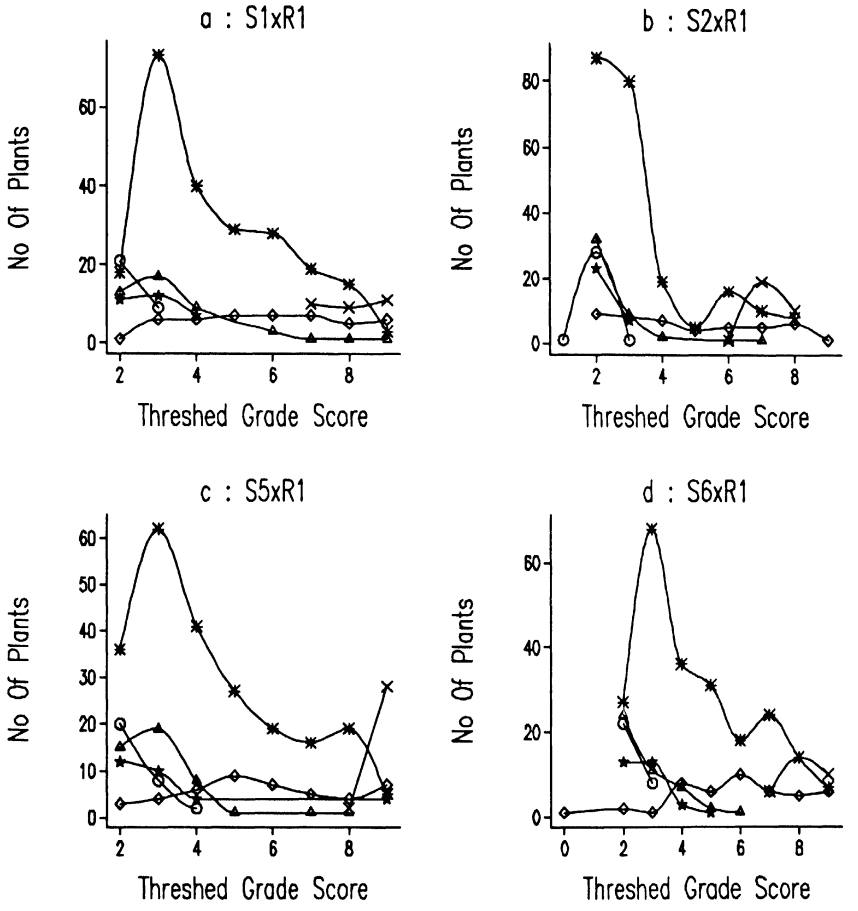


Figure 10. Frequency distributions of P_1, P_2, F_1, F_2, BC_1 and BC_2 families in different crosses of sorghum for TGS (1995).

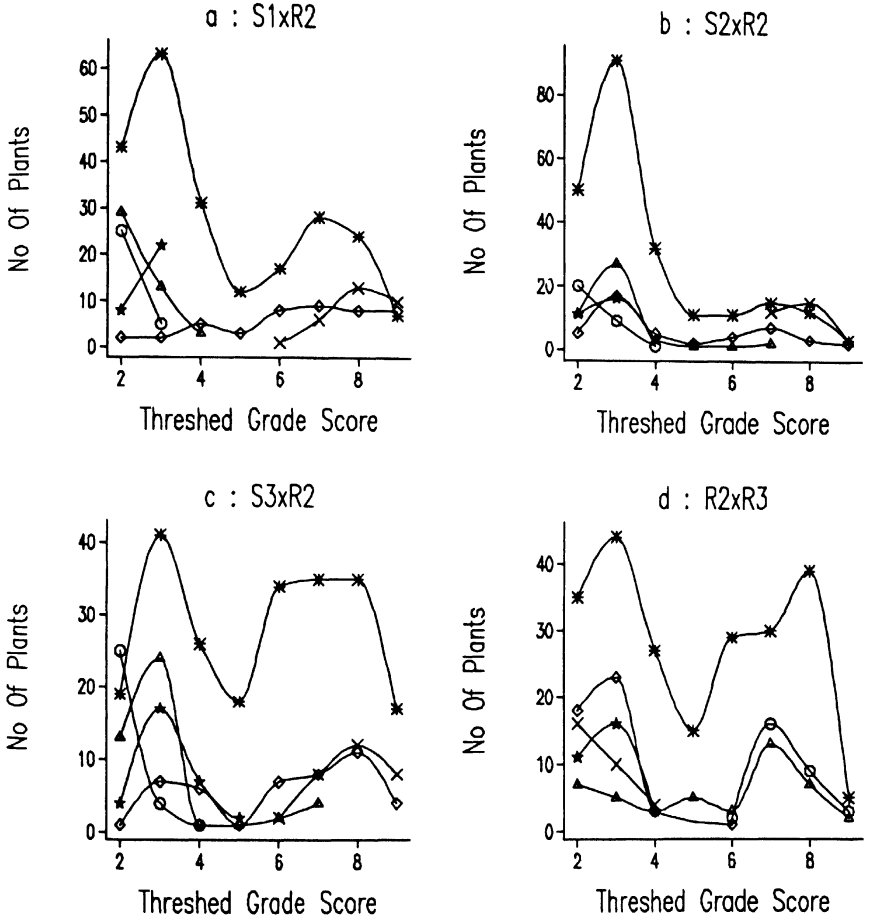


Figure 11. Frequency distributions of P_1, P_2, F_1, F_2, BC_1 and BC_2 families in different crosses of sorghum for TGS (1995).

Frequency distributions of six families for TGS in eight crosses tested during 1996, are shown in Figs 12 and 13. In six crosses $S_1 \times R_1$, $S_1 \times R_2$, $S_1 \times R_3$, $S_5 \times R_1$, $R_1 \times R_2$ and $R_2 \times R_3$, the F_2 distributions were unimodal (Figs 13 and 14). However, the distributions of F_1 were skewed towards the resistant parent and the distributions of BC_1 overlapped with those of BC_2. In $S_1 \times R_6$ and $S_1 \times R_{16}$, the F_2 distributions skewed towards high TGS values. The values of F_1 hybrids were distributed in the range of 6 to 8 (Plate 8) while the distributions of BC_1 and BC_2 overlapped with each other.

Segregation pattern: Segregation ratios for TGS in F_2, BC_1 and BC_2 generations of ten crosses were found identical to those of FGS in various crosses (Tables 12 and 17). As such, the inheritance pattern, estimates of gene number, etc., given in 4.2.1 of this chapter hold good for the data summarised in Table 17.

Generation mean analysis: Estimates of gene effects for threshed grade score in different crosses grown during 1995, are given in Table 18. Threshed grade score, similar to field grade score, showed significant additive gene effects in various crosses except $R_1 \times R_2$. Also, significant dominance gene effects were observed in five crosses, *viz.*, $S_2 \times R_1$, $S_5 \times R_1$, $S_1 \times R_2$, $S_2 \times R_2$ and $S_3 \times R_2$. Further significant dominance × dominance interactions were recorded in those crosses where dominance gene action was absent. On the other hand, in four crosses, $S_2 \times R_1$, $S_1 \times R_2$, $S_2 \times R_2$ and $R_2 \times R_3$, additive × dominance gene interactions were found significant.

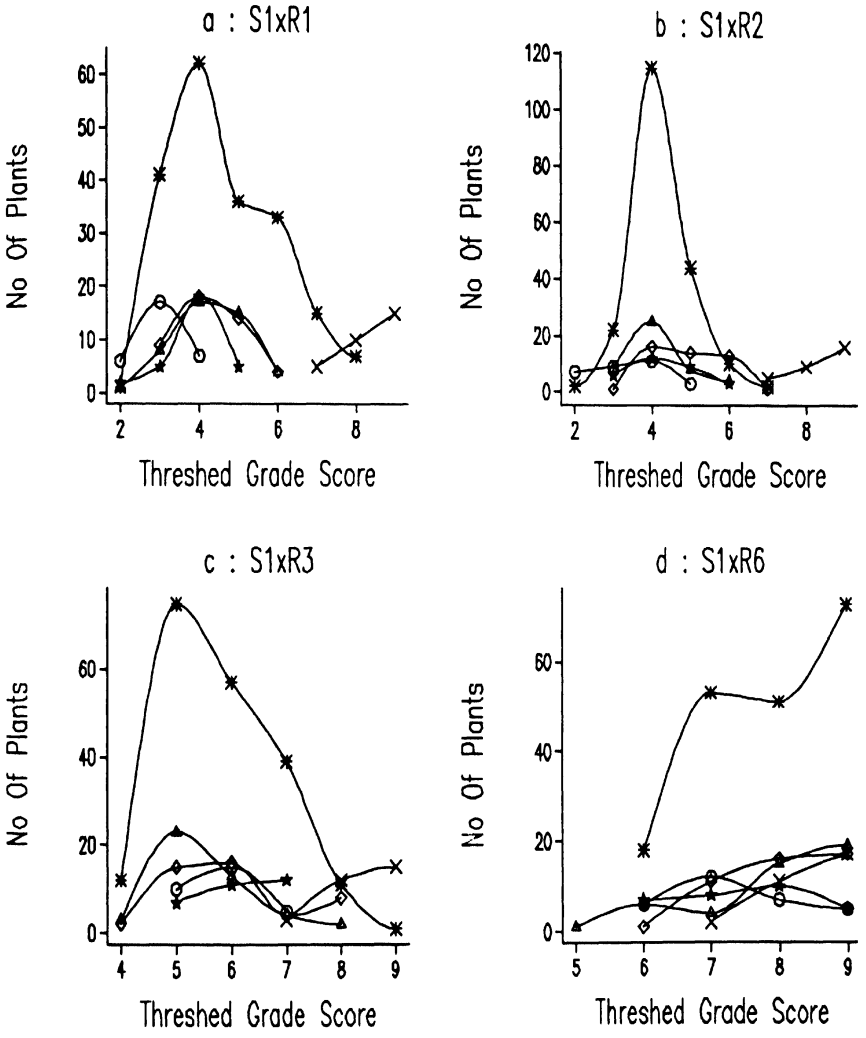


Figure 12. Frequency distributions of P_1, P_2, F_1, F_2, BC_1 and BC_2 families in different crosses of sorghum for TGS (1996).

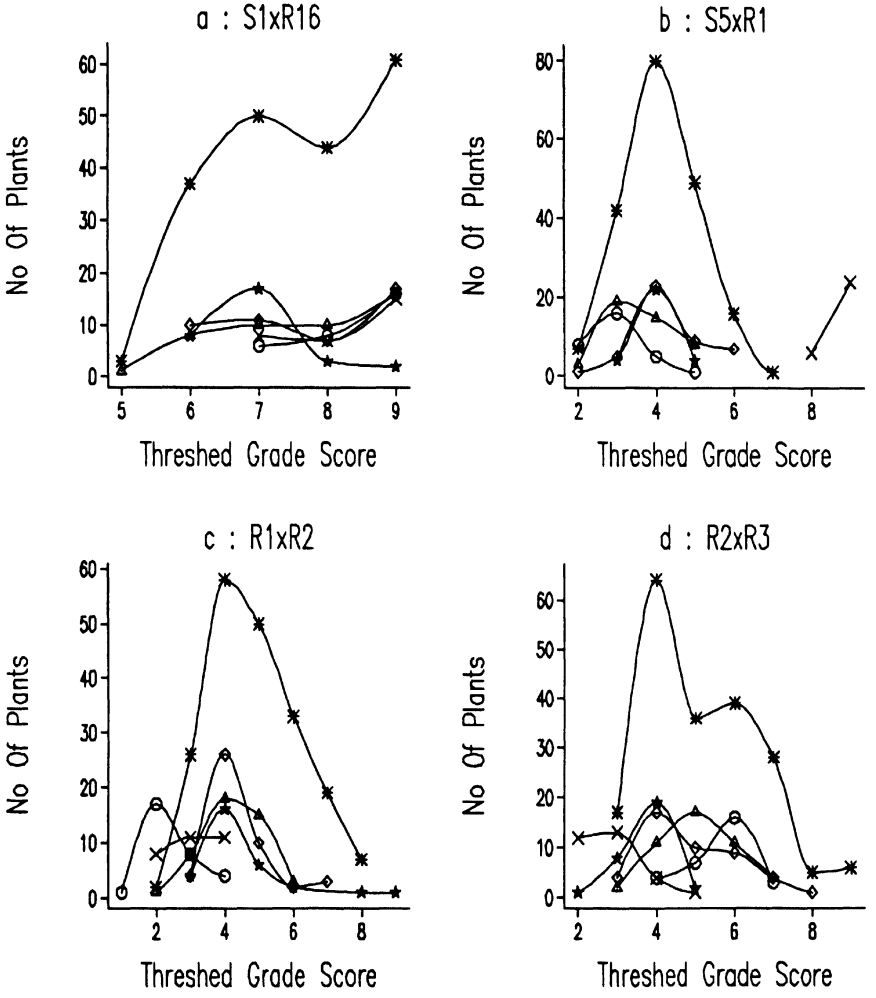


Figure 13. Frequency distributions of P_1, P_2, F_1, F_2, BC_1 and BC_2 families in different crosses of sorghum for TGS (1996).

Table 17. Segregation ratios for threshed grade score of F_2 and backcross populations derived from crosses of susceptible × resistant genotypes.

Cross	Generation	Resistant genotype(R)	Susceptible genotype(S)	Ratio	χ^2	Probability
$S_1 \times R_1$	F_2	131	94	9:7	0.35	0.70-0.05
	BC_1	11	34	1:3	0.01	0.95-0.90
$S_5 \times R_1$	F_2	139	86	9:7	2.78	0.10-0.05
	BC_1	13	32	1:3	0.36	0.70-0.50
$S_6 \times R_1$	F_2	131	94	9:7	0.35	0.70-0.50
	BC_1	12	33	1:3	0.07	0.80-0.70
$S_2 \times R_1$	F_2	186	39	51:13	1.23	0.30-0.20
	BC_1	24	21	1:1	0.28	0.70-0.50
$S_1 \times R_2$	F_2	137	88	39:25	0.00	0.98-0.95
	BC_1	9	36	1:3	0.60	0.50-0.80
$S_2 \times R_2$	F_2	173	52	45:19	4.66	0.05-0.02
	BC_1	27	18	1:1	1.10	0.30-0.20
$S_3 \times R_2$	F_2	86	139	27:37	0.86	0.50-0.30
	BC_1	7	38	1:7	0.40	0.70-0.80
$R_2 \times R_3$	F_2	106	118	27:37	2.73	0.10-0.05
	BC_2	10	35	1:7	4.00	0.05-0.02
$R_1 \times R_2$	F_2	186	24	57:7	0.44	0.90-0.80
	BC_1	37	8	1:3	1.22	0.30-0.20

R = Resistant, S = Susceptible.

Table 18. Estimates of gene effects for threshed grade score in different crosses of sorghum during 1995.

Cross	$S_1 \times R_1$	$S_2 \times R_1$	$S_5 \times R_1$	$S_6 \times R_1$	$S_1 \times R_2$	$S_2 \times R_2$	$S_3 \times R_2$	$S_1 \times R_3$	$R_2 \times R_3$	$R_1 \times R_2$
[m]	5.139*	4.594*	5.695*	5.125*	6.427*	4.999*	8.300*	8.198*	5.113*	2.837*
[d]	2.834*	2.596*	3.231*	2.915*	2.916*	2.646*	2.811*	0.242*	-2.377*	
[h]		-2.369*	-2.447*		-3.680*	-2.301*	-6.140*			
[i]					-1.339*		-3.283*			0.775*
[j]		1.230*			1.632*	-2.347*			-2.185*	
[l]	-2.284*			-2.440*			1.07		-2.218*	
R^2	99.60	99.71	99.82	99.43	99.05	99.9	100.0	81.43	95.43	89.8

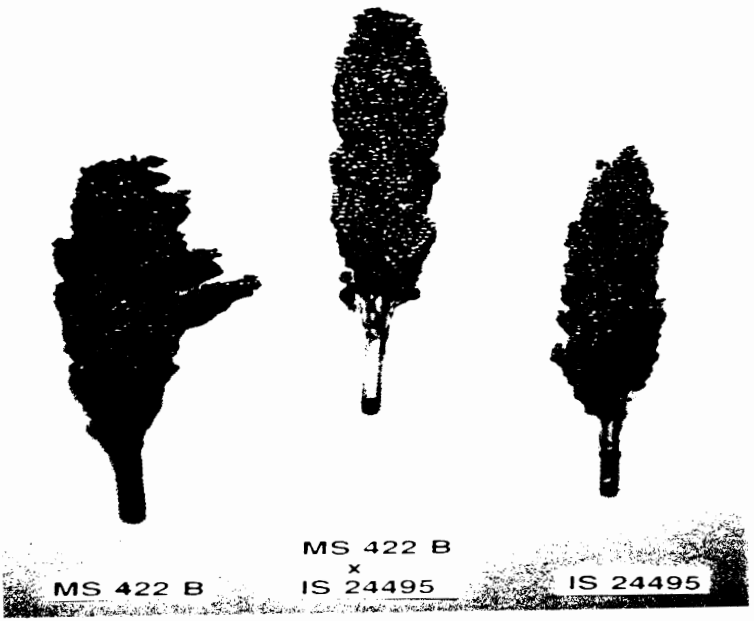
* Significant at p = 0.05

Plate 8. Parents and F_1 of white susceptible x white moderately resistant crosses.

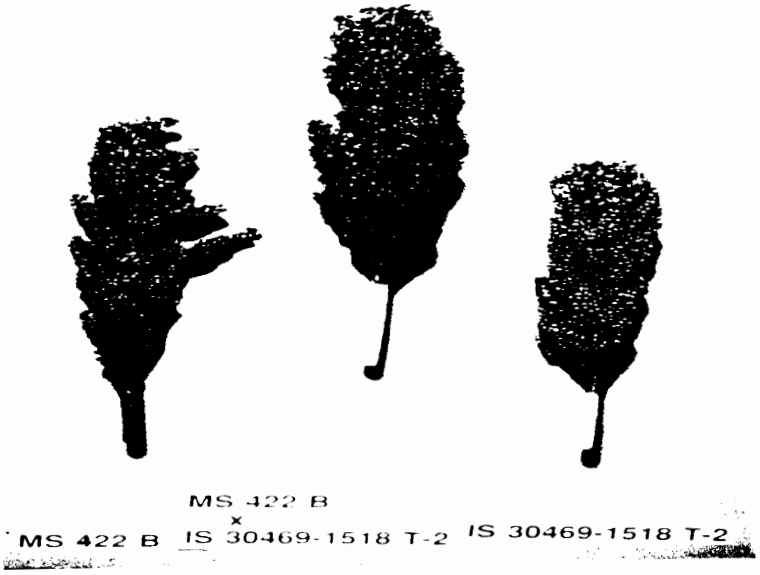
A: White susceptible (MS 422B), moderately resistant F_1 and white moderately resistant (IS 24495).

B: White susceptible (MS 422B), moderately resistant F_1 and white moderately resistant (IS 30469-15187-2).

Plate 8


MS 422 B
MS 422 B
x
IS 24495
IS 24495

A


MS 422 B
x
MS 422 B
IS 30469-1518 T-2
IS 30469-1518 T-2

B

Estimates of gene effects for TGS in different crosses grown during 1996 are given in Table 19. In most of the crosses, except $S_1 \times R_{16}$, significant additive gene effects were observed. In the crosses $S_1 \times R_1$ and $S_1 \times R_{16}$ significant negative dominance effects were recorded. In four crosses $S_1 \times R_1$, $S_1 \times R_2$, $S_1 \times R_3$ and $S_5 \times R_1$, significant additive × dominance interactions were observed.

Genotype × Environment (G×E) interactions: Estimates of G×E interactions for pooled data of 1995 and 1996, in six crosses, for FGS and TGS, are given in Tables 20 and 21. For both the variables, the various crosses showed significant additive gene effects. Significant dominant gene effects were also observed in most of the crosses. Environmental, environmental × additive and environmental × dominance components, in general, were of lesser magnitude. In the cross $S_1 \times R_3$, environmental effects, environment × additive (e × d) and environment × dominance (e × h) interactions were found significant and substantial. In $R_2 \times R_3$, substantial e × d and e × h interactions were observed, and in $R_1 \times R_2$, e × h interactions were recorded both for FGS and TGS.

4.3 GENETIC ANALYSIS OF MORPHOLOGICAL CHARACTERS IN DIFFERENT CROSSES OF SORGHUM

4.3.1. Days to flowering

Table 19. Estimates of gene effects for threshed grade score in different crosses of sorghum during 1996.

Cross	$S_1 \times R_1$	$S_1 \times R_2$	$S_1 \times R_3$	$S_1 \times R_6$	$S_1 \times R_{16}$	$S_5 \times R_1$	$R_1 \times R_2$	$R_2 \times R_3$
[m]	5.66*	4.12*	5.78*	8.05*	8.30*	3.99*	4.83*	4.52*
[d]	2.63*	2.46*	1.39*	0.45*		2.70*	0.29*	-1.24*
[h]	-2.95*				-1.31*			
[i]		1.67*	1.19*			1.57*	-2.02*	
[j]	-5.31*	-3.39*	-1.52*			-3.77*		
[l]	1.15*			-0.53*				
R^2	95.07	99.68	92.30	78.51	98.92	86.32	98.28	45.18

* Significant at p = 0.05

Table 20. Estimates of G × E effects for field grade score in sorghum during 1995 and 1996.

Cross	$S_1 \times R_1$	$S_1 \times R_2$	$S_1 \times R_3$	$S_5 \times R_1$	$R_2 \times R_3$	$R_1 \times R_2$
[m]	5.75*	5.87*	7.86*	5.83*	5.07*	2.80*
[d]	2.52*	2.68*	0.87*	2.57*	-2.23*	0.14*
[h]	-2.28*	-2.08*	-0.89*	-1.72*	2.00*	
[e]		-0.17*	0.64*			-0.33*
[exd]	0.52*	0.53*	-0.39*	0.62*	-0.78*	
[exh]	-0.33*		0.91*	-0.40*	-0.92*	-1.07*
R^2	84.7	89.0	92.6	97.0	91.3	80.0

* Significant at p = 0.05

Table 21. Estimates of G x E effects for threshed grade score in sorghum during 1995 and 1996.

Cross	$S_1 \times R_1$	$S_1 \times R_2$	$S_1 \times R_3$	$S_5 \times R_1$	$R_2 \times R_3$	$R_1 \times R_2$
[m]	5.43*	5.50*	7.52*	5.34*	4.78*	2.76*
[d]	2.41*	2.49*	0.77*	2.53*	-1.99*	0.18*
[h]	-2.03*	-2.47*	-0.79*	-1.91*	-0.90*	1.61*
[e]		-0.22*	0.74*	0.45*		-0.28*
[exd]	0.34*	0.47*	-0.53*	0.60*	-0.75*	
[exh]	-0.27*		0.67*	-0.73*	-0.42*	-1.13*
R^2	84.7	89.0	92.6	97.0	91.3	84.0

* Significant at p = 0.05

Family means: In nine out of ten crosses, during 1995, the F_1 means tended towards the early parent (Table 22). Also the mean values of BC_1, BC_2 and F_2 tended towards the mean of the early parent. However, in one cross, $S_1 \times R_3$, while the F_1 and BC_2 means were close to the mid-parent value, the BC_1 and F_2 means tended towards the early parent.

Means of the six families in different crosses for days to flowering, grown during 1996, are given in Table 23. In the crosses, $S_1 \times R_1$, $S_1 \times R_2$, $S_1 \times R_6$ and $R_1 \times R_2$, the F_1 and BC_1 means were similar. On the other hand, in crosses, $S_1 \times R_1$, $S_1 \times R_2$ and $R_1 \times R_2$, the F_1 mean tended towards the early parent. However in two crosses, $S_1 \times R_3$ and $S_1 \times R_6$, the F_1 means were similar to the mid-parent value. In two other crosses, $S_1 \times R_{16}$ and $S_5 \times R_1$, the F_1 means tended towards the late parent.

Frequency distributions: Frequency distributions in six families for days to flowering in ten crosses, grown during 1995, are depicted in Figs 14 to 16. In two crosses, $S_1 \times R_1$ and $R_1 \times R_2$, the F_2 distributions were bimodal (Figs 15a and 14a). In three crosses, $S_5 \times R_1$, $R_2 \times R_3$, and $S_3 \times R_2$ (Figs 15c, 16c, and 16d), the F_2 distributions showed trimodal pattern. While in five crosses, $S_6 \times R_1$, $S_1 \times R_3$ $S_1 \times R_2$, $S_2 \times R_1$, and $S_2 \times R_2$ (Figs 14, 15 and 16), the F_2 distributions showed four to five modes. In all ten crosses, the distributions of F_1, BC_1 and BC_2 overlapped with those of early parent.

Table 22. Means of the six families for days to flower in different crosses of sorghum during 1995.

Families		$S_1 \times R_1$	$S_2 \times R_1$	$S_5 \times R_1$	$S_6 \times R_1$	$S_1 \times R_2$	$S_2 \times R_2$	$S_3 \times R_2$	$S_1 \times R_3$	$R_2 \times R_3$	$R_1 \times R_2$
P_1	M	65.20	63.20	61.80	64.30	65.10	63.50	65.40	65.40	70.20	74.40
	SE	0.77	0.31	0.37	0.13	0.34	0.34	0.44	0.31	0.63	0.44
P_2	M	73.90	75.20	75.00	73.70	70.70	73.20	69.70	77.20	76.20	70.30
	SE	0.63	0.40	0.40	0.53	0.32	0.43	0.52	0.22	0.50	0.38
F_1	M	65.60	65.50	65.50	65.90	64.70	64.20	64.40	70.60	69.60	71.00
	SE	0.72	0.54	0.72	0.56	0.35	0.48	0.50	0.32	0.45	0.34
BC_1	M	65.60	63.60	61.40	62.90	66.10	63.20	63.30	67.30	69.70	70.50
	SE	0.56	0.75	0.79	0.62	0.53	0.60	0.56	0.45	0.42	0.36
BC_2	M	66.60	68.10	69.70	68.10	66.70	65.30	62.40	70.30	71.40	71.80
	SE	0.64	0.54	0.56	0.65	0.57	0.60	0.48	0.64	0.52	0.29
F_2	M	67.40	65.10	65.90	64.10	65.50	63.80	63.10	68.80	72.40	72.40
	SE	0.47	0.46	0.49	0.44	0.34	0.39	0.44	0.38	0.26	0.16

M = Mean, SE = Standard error.

Table 23. Means of the families for days to flower in different crosses of sorghum in 1996.

Families		$S_1 \times R_1$	$S_1 \times R_2$	$S_1 \times R_3$	$S_1 \times R_6$	$S_1 \times R_{16}$	$S_5 \times R_1$	$R_1 \times R_2$	$R_2 \times R_3$
P_1	M	72.83	71.20	71.70	72.50	70.03	66.43	81.47	75.50
	SE	0.87	0.35	0.38	0.53	0.23	0.60	0.45	0.74
P_2	M	80.03	76.43	83.10	73.00	67.33	80.00	76.93	82.47
	SE	0.88	0.38	0.27	0.69	0.73	0.72	0.75	0.27
F_1	M	71.30	71.10	78.93	71.57	69.50	78.33	78.73	78.00
	SE	0.61	0.45	0.60	0.46	0.61	0.67	0.56	0.68
BC_1	M	71.49	71.00	72.51	70.40	70.04	72.60	79.20	75.89
	SE	0.51	0.36	0.69	0.50	0.62	0.52	0.68	0.64
BC_2	M	77.22	79.29	78.51	70.93	69.58	77.07	76.64	81.07
	SE	0.95	0.40	0.42	0.53	0.74	0.55	0.68	0.38
F_2	M	77.71	77.40	77.21	71.82	69.31	76.84	80.97	79.25
	SE	0.41	0.23	0.23	0.23	0.29	0.26	0.21	0.27

M = Mean, SE = Standard error.

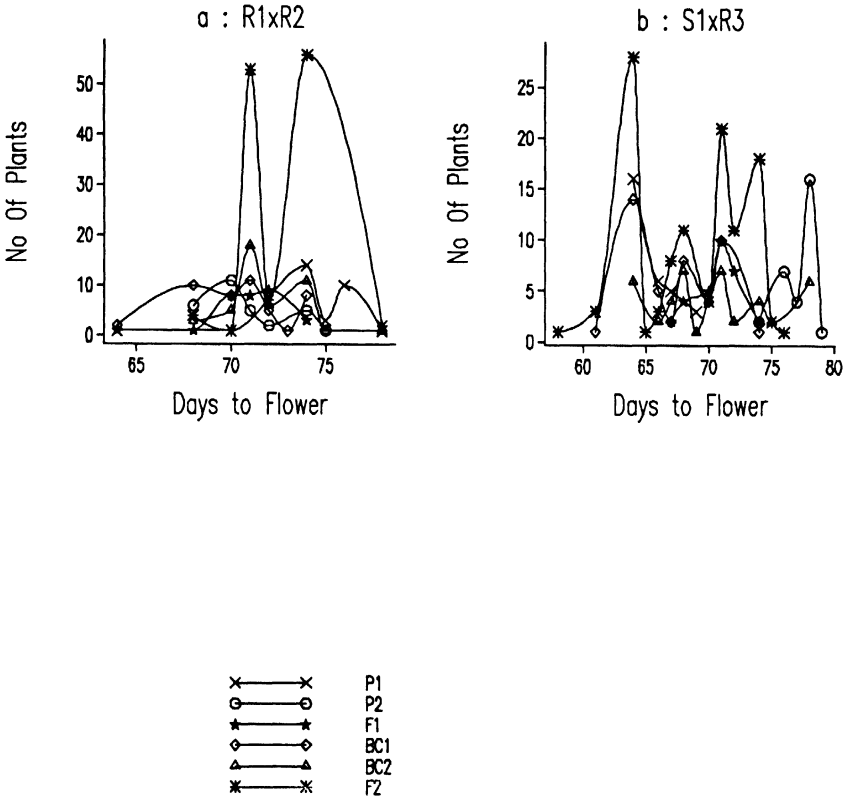


Figure 14. Frequency distributions of P_1, P_2, F_1, F_2, BC_1 and BC_2 families in different crosses of sorghum for DF (1995).

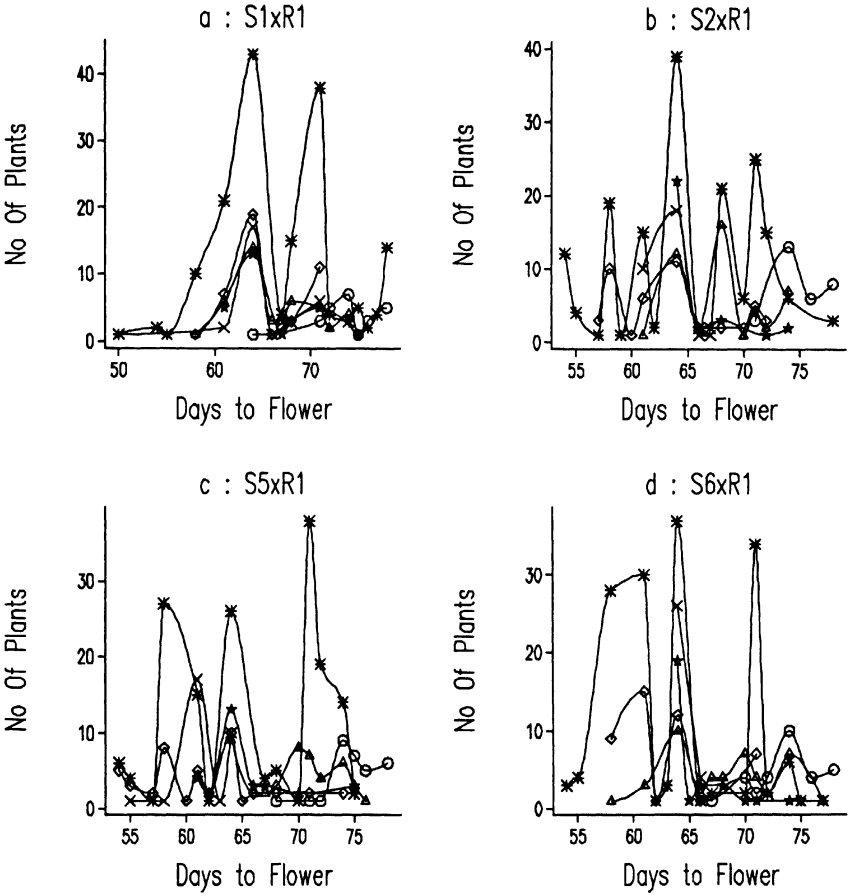


Figure 15. Frequency distributions of P_1, P_2, F_1, F_2, BC_1 and BC_2 families in different crosses of sorghum for DF (1995).

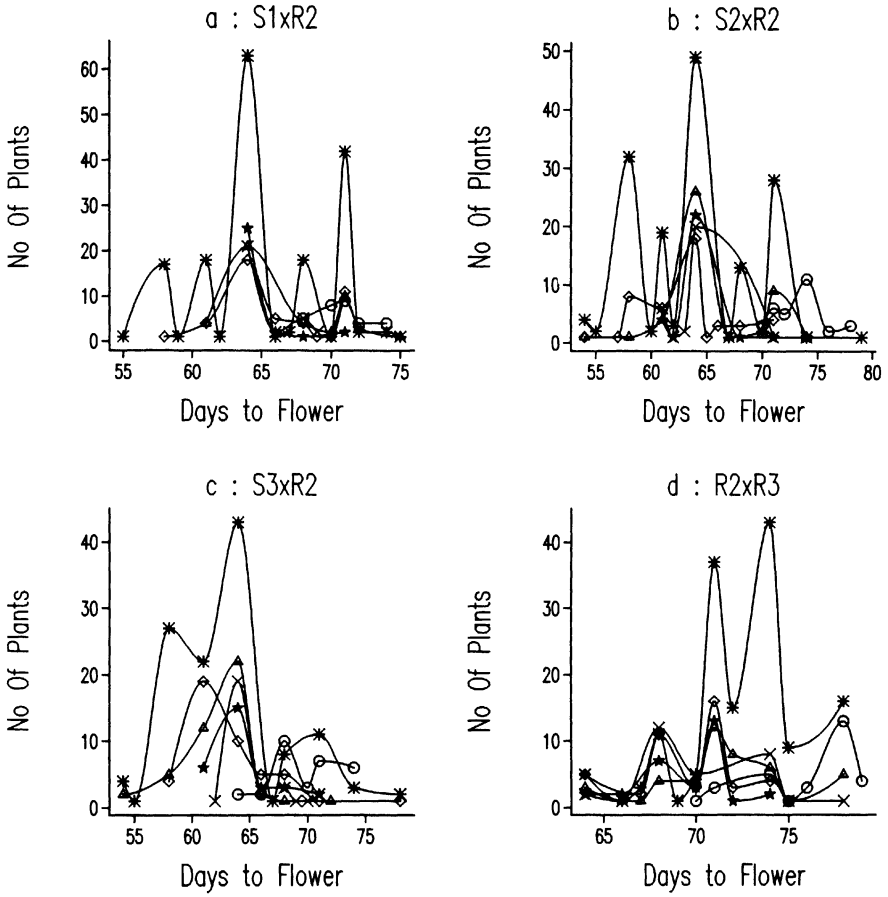


Figure 16. Frequency distributions of P_1, P_2, F_1, F_2, BC_1 and BC_2 families in different crosses of sorghum for DF (1995).

In F_2 and BC_1 families differential transgressive segregants for earliness were obtained.

Frequency distributions in six families, for days to flowering, of eight crosses during 1996 are shown in Figs 17 and 18. In three crosses, $S_1 \times R_1$, $R_2 \times R_3$ and $R_1 \times R_2$, the F_2 distributions were bimodal (Figs 17 and 18). On the other hand, in three crosses, $S_1 \times R_2$, $S_1 \times R_3$ and $S_5 \times R_1$, trimodal distributions were observed. However, in two crosses, $S_1 \times R_6$, $S_1 \times R_{16}$, four peaks were observed for the F_2 distributions. In two crosses, $S_1 \times R_1$ and $S_1 \times R_2$, the distributions of F_1 and BC_1 overlapped with those of the early parent and the distributions of BC_2 overlapped with those of recurrent parent. On the other hand, in six crosses, $S_1 \times R_3$, $S_1 \times R_6$, $S_1 \times R_{16}$, $S_5 \times R_1$, $R_1 \times R_2$ and $R_2 \times R_3$, the F_1 distributions ranged between the parents. Whereas in three crosses, $S_1 \times R_{16}$, $R_1 \times R_2$ and $R_2 \times R_3$, the mode of the distribution tended towards the early parent, in two crosses, $S_1 \times R_3$ and $S_5 \times R_1$, it was intermediate. However, in one cross $S_1 \times R_6$ the mode in F_1 distribution was earlier than those of the early parent.

Generation mean analysis: Estimates of gene effects for days to flowering during 1995 are given in Table 24. In all the crosses, except $R_1 \times R_2$ and $S_3 \times R_2$, the R^2 values were high (76 to 100%). In various crosses, additive gene effects and its first order interaction, additive × additive gene interaction were found predominant. In six crosses, estimates of additive × dominance gene interactions were more important.

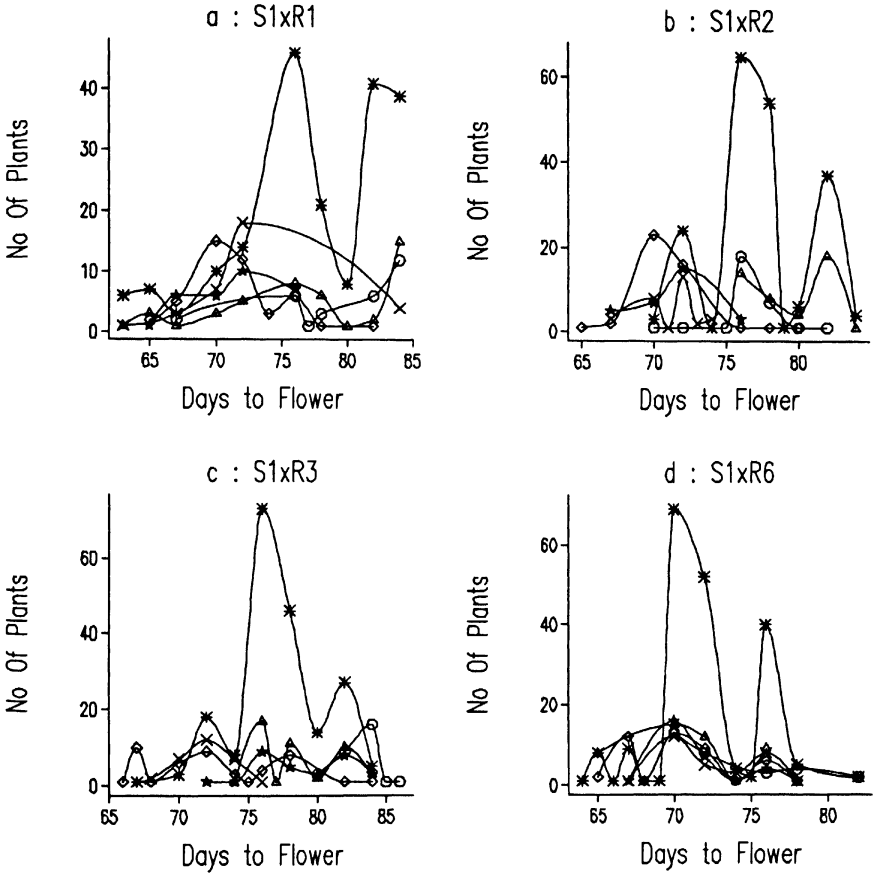


Figure 17. Frequency distributions of P_1, P_2, F_1, F_2, BC_1 and BC_2 familes in different crosses of sorghum for DF (1996).

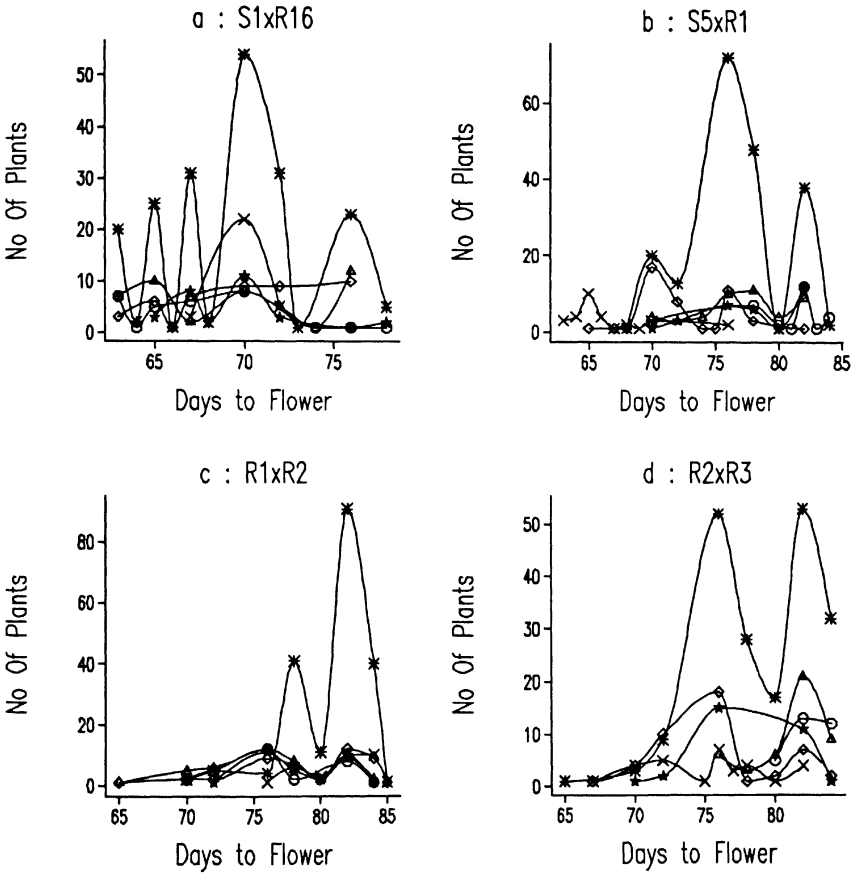


Figure 18. Frequency distributions of P_1, P_2, F_1, F_2, BC_1 and BC_2 families in different crosses of sorghum for DF (1996).

Table 24. Estimates of gene effects for days to flower in sorghum during 1995.

Cross	$S_1 \times R_1$	$S_2 \times R_1$	$S_5 \times R_1$	$S_6 \times R_1$	$S_1 \times R_2$	$S_2 \times R_2$	$S_3 \times R_2$	$S_1 \times R_3$	$R_2 \times R_3$	$R_1 \times R_2$
[m]	69.16*	65.06*	65.52*	63.60*	65.26*	63.73*	61.63*	67.73*	74.95*	72.44*
[d]	-4.44*	-5.87*	-6.71*	-4.76*	-2.82*	-4.84*	-2.13*	-5.90*	-2.84*	1.83*
[h]	-4.35*								-5.74*	
[i]		4.04*	2.84	5.43*	2.73*	4.56*	5.73*	3.53*	-2.05*	
[j]	6.39*				4.67*	5.42*	6.58*	5.12*	-5.43*	
[l]				2.30*			2.72*	2.85*		-1.50*
R^2	86.85	98.94	99.01	99.77	95.24	98.02	66.19	98.97	75.99	32.28

* significant at p = 0.05

Estimates of gene effects in seven crosses, grown during 1996, are given in Table 25. In three crosses, $S_1 \times R_1$, $S_1 \times R_2$, and $S_1 \times R_{16}$, the R^2 values varied from 39 to 67%, whereas substantial R^2 values (91 to 100%) were obtained in the remaining crosses. The results indicate that additive gene effects were important and significant in most of the crosses. However, in one cross, $R_1 \times R_2$, dominance and dominance × dominance interaction were more important.

4.3.2 Seed colour

Family means: In four white × red crosses, $S_1 \times R_1$, $S_2 \times R_1$, $S_5 \times R_1$ and $S_6 \times R_1$, the F_1 means were greater than those of both the parents (Table 26). Although the BC_1 means tended towards the red parent, the BC_2 and F_2 means were greater than those of red parent.

However, in white × brown crosses, $S_1 \times R_2$, $S_2 \times R_2$ and $S_3 \times R_2$, the F_1 means (score 7.2 to 7.9) were less than those of the brown parent (score 8). The means of BC_1 and BC_2 tended towards recurrent parents and the F_2 means were less than those of the brown parent.

On the other hand, in the brown (R_2) × white (R_3) cross, the F_1 and BC_1 means tended towards the brown parent, while the BC_2 mean tended towards the mid-parent value. However, in the red (R_1) × brown (R_2) cross, the F_1 mean was greater

Table 25. Estimates of gene effects for days to flower in sorghum during 1996.

Cross	$S_1 \times R_1$	$S_1 \times R_2$	$S_1 \times R_3$	$S_1 \times R_{16}$	$S_5 \times R_1$	$R_1 \times R_2$	$R_2 \times R_3$
[m]	77.24*	75.19*	77.13*	69.25*	76.76*	91.38*	78.93*
[d]	- 4.81*	-2.76*	- 5.67*	0.87*	- 6.12*	2.32*	- 3.68*
[h]						-28.99*	
[i]					- 3.99*	-12.20*	
[j]		-11.07*					
[l]	- 5.69*					16.34*	
R^2	59.06	39.06*	94.75	67.22	91.23	99.51	94.75

* Significant at p = 0.05

Table 26. Means of the six families for seed colour in different crosses of sorghum during 1995.

Families		S_1xR_1	S_2xR1	S_5xR_1	S_6xR_1	S_1xR_2	S_2xR_2	S_3xR_2	S_1xR_3	R_2xR_3	R_1xR_2
P_1	M	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	8.00	5.00
	SE	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
P_2	M	5.00	5.00	5.00	5.00	8.00	7.80	8.00	1.00	1.00	8.00
	SE	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
F_1	M	9.90	10.00	10.00	10.00	7.20	7.80	7.20	1.00	7.90	9.40
	SE	0.09	0.00	0.00	0.00	0.14	0.07	0.07	0.00	0.06	0.21
B_1	M	4.50	5.60	5.70	5.80	3.10	5.40	3.40	1.00	7.70	6.30
	SE	0.45	0.49	0.46	0.49	0.44	0.49	0.45	0.00	0.12	0.49
B_2	M	6.10	6.40	6.30	5.80	7.10	7.40	6.40	1.00	3.80	7.50
	SE	0.42	0.37	0.37	0.39	0.22	0.26	0.34	0.00	0.49	0.34
F_2	M	6.00	6.00	6.10	6.10	5.70	6.30	4.10	1.00	4.70	6.80
	SE	0.20	0.19	0.16	0.18	0.39	0.19	0.21	0.00	0.23	0.19

M = Mean, SE = Standard error.

than those of both the parents. The BC_1 and F_2 means tended towards the mid-parent value and that of BC_2 tended towards the brown parent.

Frequency distributions: Frequency distributions of six families for seed colour are depicted in Figs 19 to 21. In all ten crosses, the F_2 distributions showed unimodal pattern with 2 to 3 peaks. In the white × red and red × brown crosses (Figs 19 and 20), the F_2 distributions skewed towards the red parent (score 5). In white × red crosses (Fig. 20), except in $R_1 \times R_2$, the BC_1 distribution spread between those of P_1, P_2 and F_1. The BC_2 distributions were similar to those of the F_2 showing maximum peak at score 5 (red colour). The BC_1 and BC_2 distributions overlapped at the score 5 (red) and BC_2 distributions showed a second peak at score 8 (brown). Also, in white × brown crosses, F_2 distributions (Fig. 21) were unimodal, the maximum peak being at score 8. The F_1 distributions overlapped those of P_2 (the brown parent), while the BC_1 distribution was spread between two parents. Likewise, BC_2 distribution also was spread from white parent to F_1 (score 1 to 10).

Generation mean analysis: In different crosses substantial dominant gene effects were observed which were greater in magnitude than additive gene effects (Table 27). In four crosses, $S_1 \times R_1$, $S_1 \times R_2$, $S_2 \times R_2$ and $R_2 \times R_3$, additive gene effects were found significant. On the other hand, in $S_1 \times R_1$, $S_2 \times R_1$, $S_5 \times R_1$, $R_1 \times R_2$ and $S_1 \times R_2$, dominance × dominance gene interactions were found significant. In three crosses, $S_2 \times R_1$, $S_2 \times R_2$ and $R_2 \times R_3$ additive × dominance gene interactions were significant.

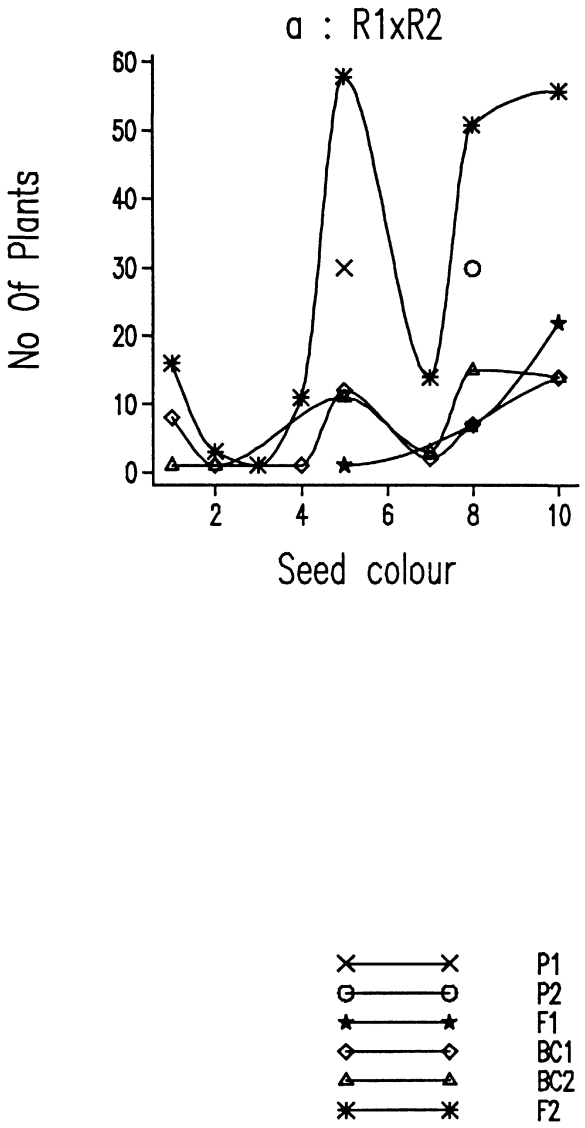


Figure 19. Frequency distributions of P_1, P_2, F_1, F_2, BC_1 and BC_2 families in R_1xR_2 cross for seed colour (1995).

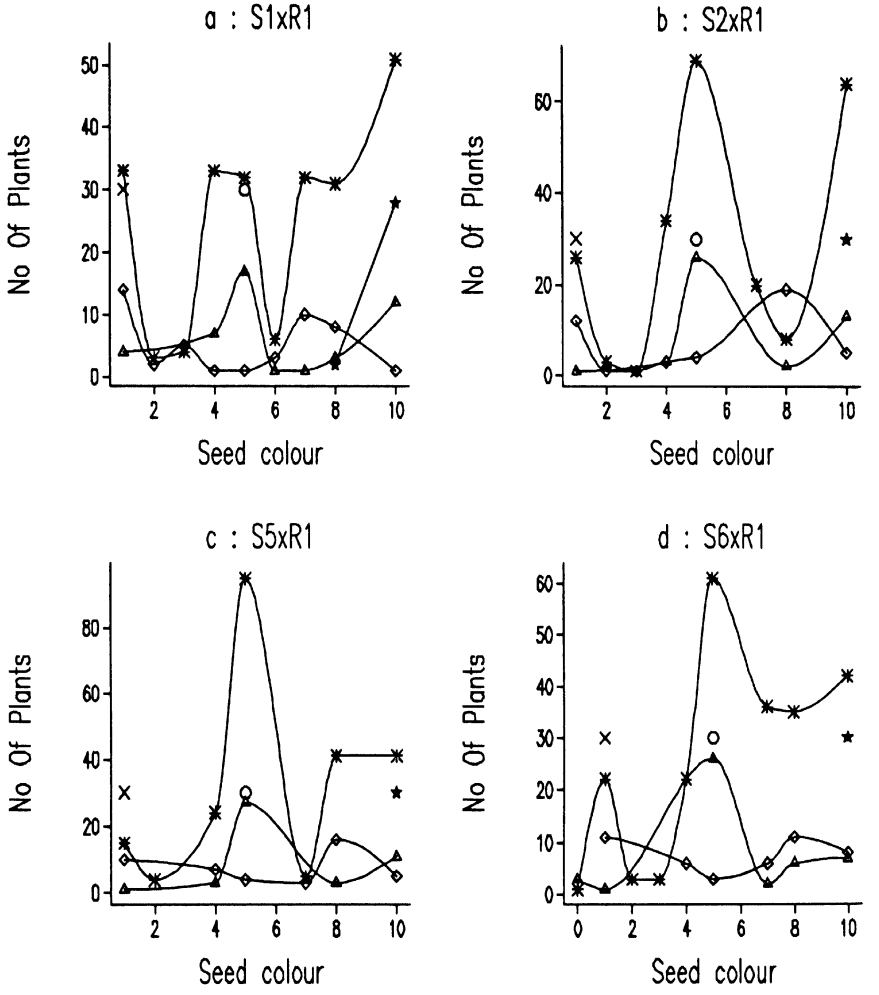


Figure 20. Frequency distributions of P_1, P_2, F_1, F_2, BC_1 and BC_2 families in different crosses of sorghum for seed colour (1995).

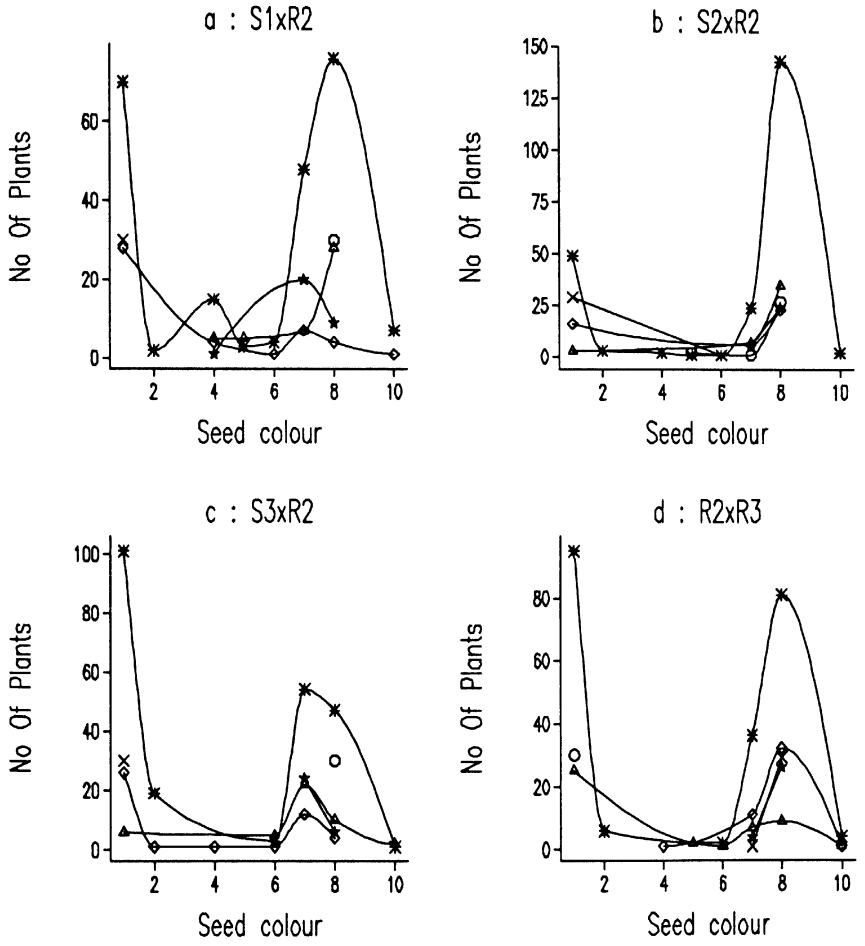


Figure 21. Frequency distributions of P_1, P_2, F_1, F_2, BC_1 and BC_2 families in different crosses of sorghum for seed colour (1995).

Table 27. Estimates of gene effects for seed colour in different crosses of sorghum during 1995.

Cross	$S_1 \times R_1$	$S_2 \times R_1$	$S_5 \times R_1$	$S_1 \times R_1$	$S_2 \times R_2$	$S_3 \times R_2$	$R_2 \times R_3$	$R_1 \times R_2$
[m]	3.00*	3.00*	3.00*	4.50*	4.47*	0.97*	1.80*	6.50
[d]	-2.00*	-2.00	-2.00	-3.50*	-3.30*	-3.50	3.48*	-1.50
[h]	4.42*	5.13*	5.22*	0.60*	3.96*	6.23*	6.08*	-1.62*
[i]						3.53*	2.69*	
[j]		2.35*	2.96*		2.41*	0.99	1.74*	
[l]	2.47*	1.88*	1.78*	2.09	-0.63			4.48
R^2	97.37	96.24	63.50	94.42	99.95	99.97	97.62	99.23

* Significant at p = 0.05

4.3.3 Percentage glume cover

Family means: In all the crosses, except $S_1 \times R_3$, (Table 28) the F_1, BC_1, and BC_2 mean values were greater than those of both the parents. However, in $S_1 \times R_3$, the means of F_1, BC_1, BC_2 and F_2 tended towards larger parent (P_1). Further, the means of BC_1 and the F_2 were not significantly different.

Frequency distributions: Frequency distributions in families, for glume cover, are shown in Figs 22 to 24. In three crosses, $S_1 \times R_1$, $S_2 \times R_1$, and $S_6 \times R_1$ (Fig. 23), the F_2 distributions showed bimodal pattern. However, the distributions of F_1 and BC_2 overlapped with those of P_2, while BC_1 distributions overlapped with those of P_1.

On the other hand, in seven crosses, $S_1 \times R_3$, $S_5 \times R_1$, $S_1 \times R_2$, $S_2 \times R_2$, $S_3 \times R_2$, $R_2 \times R_3$ and $R_1 \times R_2$, the F_2 distributions were more or less normal and symmetrical. The F_1 distributions, in general, skewed towards the larger parent, and BC_1 distributions overlapped with those of P_1 and P_2.

Generation mean analysis: In nine out of ten crosses, R^2 values were very high. In one cross, $S_1 \times R_3$, low R^2 value of 31% was obtained (Table 29). In general, additive and dominance genetic effects were significant, but the net dominance effect was greater in magnitude than the net additive gene effects (Table 29). In six

Table 28. **Means of the six families for percentage glume cover in different crosses of sorghum during 1995.**

Families		S_1xR_1	S_2xR1	S_5xR_1	S_6xR_1	S_1xR_2	S_2xR_2	S_3xR_2	S_1xR_3	R_2xR_3	R_1xR_2
P_1	M	50.00	26.70	25.00	25.00	50.00	25.00	33.30	50.00	50.80	64.70
	SE	00.00	01.67	00.00	00.00	00.00	00.00	02.18	00.00	00.83	02.43
P_2	M	53.30	50.00	50.00	50.80	55.00	50.00	66.70	25.00	25.00	67.00
	SE	01.58	00.00	00.00	00.83	02.51	00.00	02.18	00.00	00.00	02.85
F_1	M	62.20	64.20	55.80	53.30	65.00	68.00	59.70	41.70	58.30	69.30
	SE	02.47	02.30	01.96	01.57	02.27	02.24	02.41	02.19	02.18	03.17
B_1	M	66.10	56.10	50.90	47.80	68.30	58.40	54.00	45.60	62.90	66.40
	SE	02.61	02.99	02.54	02.85	02.95	02.63	02.63	01.99	02.18	02.37
B_2	M	65.30	71.30	64.80	61.10	64.60	72.60	64.00	43.90	59.70	68.90
	SE	02.07	01.90	02.09	02.17	02.29	01.75	02.50	01.62	02.89	02.81
F_2	M	65.60	61.10	67.20	58.10	71.00	64.00	59.60	45.80	60.50	69.50
	SE	01.10	01.16	01.21	02.19	01.24	01.64	01.32	00.86	01.29	01.16

M = Mean, SE = Standard error.

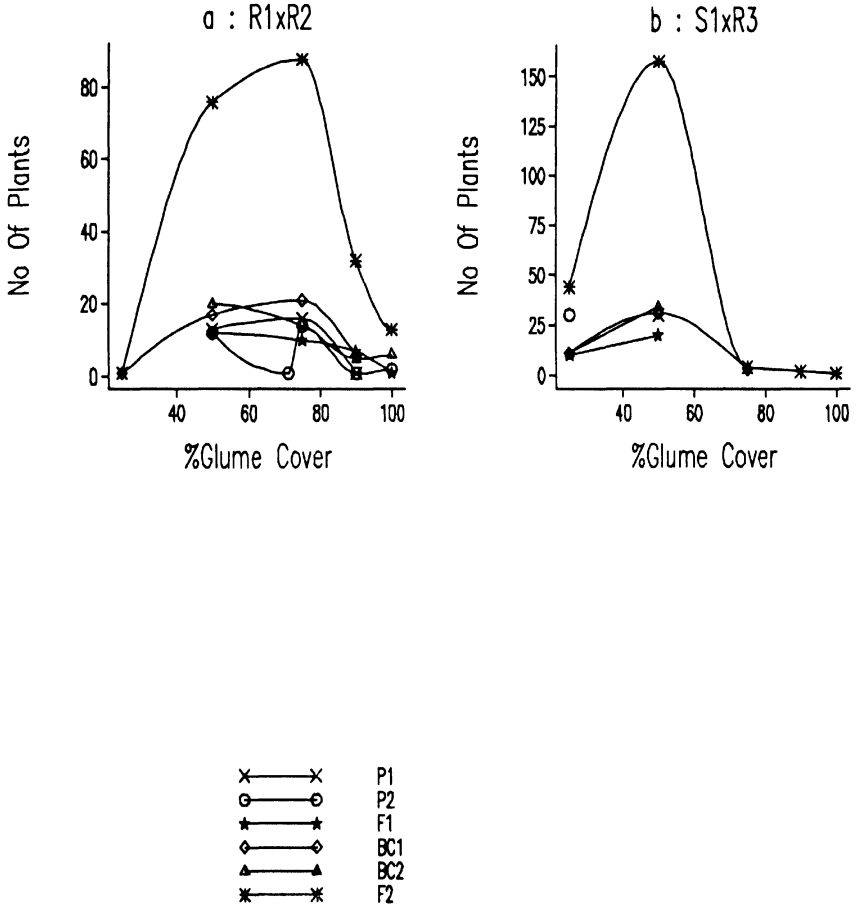


Figure 22. Frequency distributions of P_1, P_2, F_1, F_2, BC_1 and BC_2 families in different crosses of sorghum for glume cover (1995).

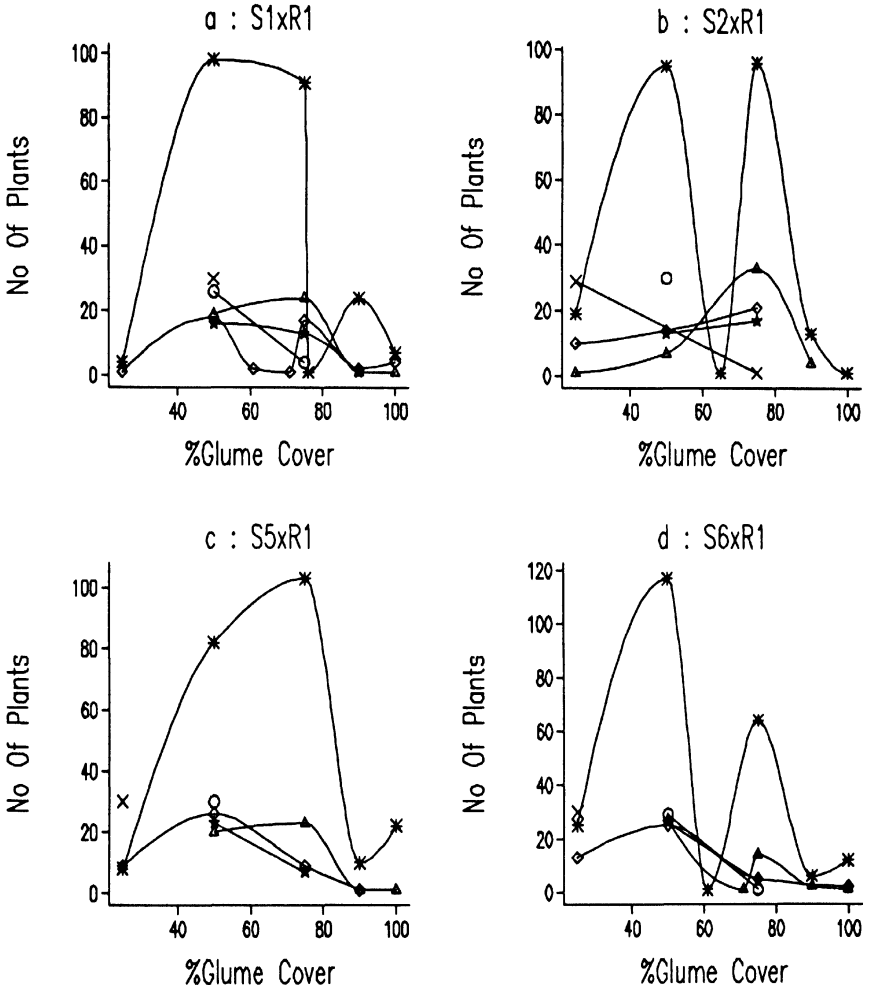


Figure 23. Frequency distributions of P_1, P_2, F_1, F_2, BC_1 and BC_2 families in different crosses of sorghum for glume cover (1995).

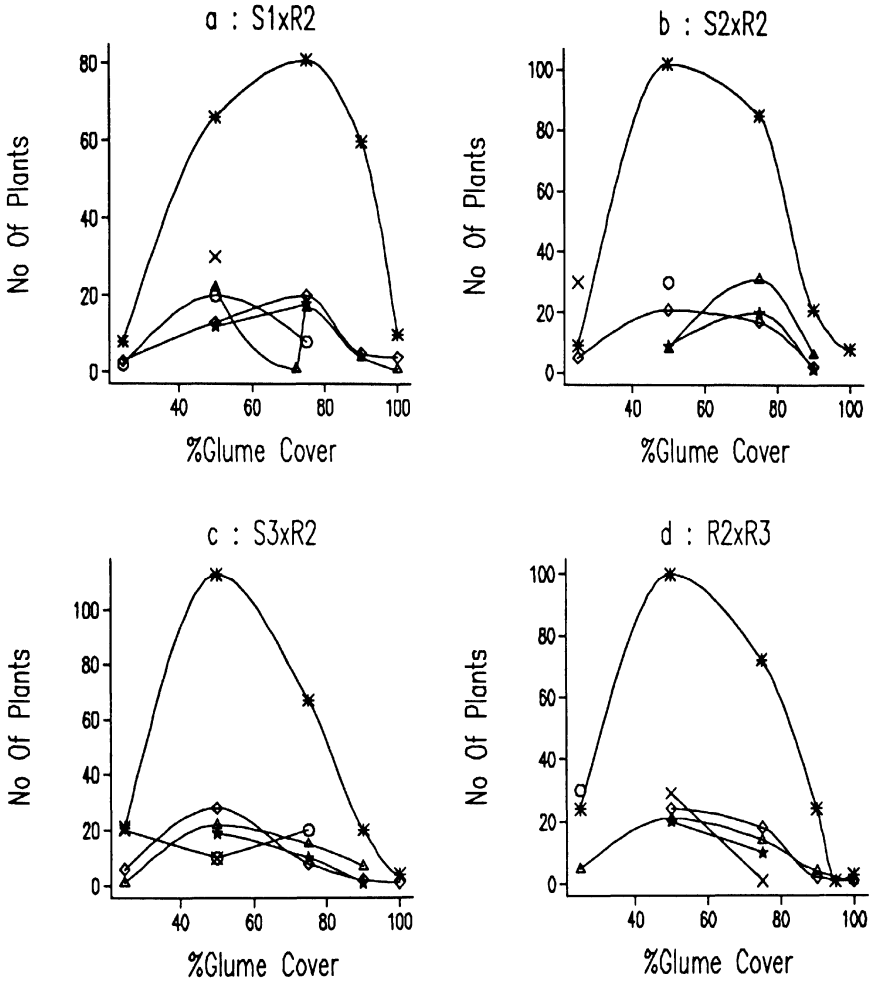


Figure 24. Frequency distributions of P_1, P_2, F_1, F_2, BC_1 and BC_2 families in different crosses of sorghum for glume cover (1995).

Table 29. **Estimates of gene effects for glume cover in different crosses of sorghum during 1995.**

Cross	$S_1 \times R_1$	$S_2 \times R_1$	$S_5 \times R_1$	$S_6 \times R_1$	$S_1 \times R_2$	$S_2 \times R_2$	$S_3 \times R_2$	$S_1 \times R_3$	$R_2 \times R_3$	$R_1 \times R_2$
[m]	51.66*	38.33*	78.74*	63.63*	77.09*	37.50	50.00*	37.50	37.91*	70.30*
[d]	- 1.66*	-11.66*	-12.50	-12.97*	- 2.65*	-12.50	-16.67*	12.50	12.92*	- 1.47
[h]	45.35*	68.52*	-22.65*	- 9.84*	-11.61*	77.50*	27.86*	27.81*	71.00*	- 1.26
[i]			-41.24*	-25.67*	-24.44*					- 4.32
[j]	4.75	-10.14	- 3.35		11.48	- 4.78	13.42	-21.03*	-18.82*	
[l]	-34.86*	-42.69*				- 4.70*	-18.19*	-23.64*	-50.59*	
R^2	99.97	98.20	97.54	87.69	91.66	88.24	99.79	31.60	99.02	81.74

* significant at p = 0.05.

of the crosses, positive dominance effects were observed; whereas, in four crosses, $S_5 \times R_1$, $S_6 \times R_1$, $S_1 \times R_2$ and $R_1 \times R_2$, negative dominance effects were noted. Also, significant negative additive × additive gene interactions were observed in three crosses in which negative dominant gene effects were noted. Further, six crosses showed significant negative dominance × dominance gene interactions.

4.3.4 Preharvest sprouting

Family means: Means of the six families for preharvest sprouting in six crosses are given in the Table 30. In one cross, *viz,* $S_1 \times R_3$ sprouting was observed in all the families. The means of the F_1 and the BC_2 families were greater than those of both the parents. Also the BC_1 and F_2 means tended towards the P_2.

Generation mean analysis: In four crosses, predominant dominant gene effects were observed for sprouting (Table 31). Out of these, two crosses, $S_5 \times R_1$ and $S_1 \times R_2$, showed negative dominance effects and negative additive × additive gene interactions. In two other crosses, $S_1 \times R_3$ and $R_2 \times R_3$ significant additive gene effects were noted. Additive × dominance interactions were found predominant in most of the crosses. Further, in $S_1 \times R_1$, $S_1 \times R_2$ and $S_1 \times R_3$, important dominance × dominance interactions were noted.

Table 30. Means of six families for preharvest sprouting in different crosses of sorghum during 1995.

Familiy		$S_1 \times R_1$	$S_5 \times R_1$	$S_1 \times R_2$	$S_3 \times R_2$	$S_1 \times R_3$	$R_2 \times R_3$
P_1	M	0.66	0.00	1.00	0.00	4.67	0.00
	SE	0.00	0.00	0.55	0.00	3.38	0.00
P_2	M	0.00	0.00	0.33	0.00	18.50	9.17
	SE	0.00	0.00	0.33	0.00	4.30	2.90
F_1	M	0.00	0.00	0.00	0.83	55.67	0.00
	SE	0.00	0.00	0.00	0.83	6.41	0.00
B_1	M	7.44	0.44	10.44	4.00	19.00	0.00
	SE	1.41	0.44	3.29	1.89	4.69	0.22
B_2	M	0.00	2.22	0.00	0.00	28.11	9.78
	SE	0.00	0.52	0.00	0.00	5.44	2.96
F_2	M	2.60	4.84	4.48	4.41	22.79	3.64
	SE	0.60	1.24	0.98	0.99	2.15	0.84

M = Mean, SE = Standard error.

Table 31. Estimates of gene effects for preharvest sprouting in different crosses of sorghum during 1995.

Cross	$S_1 \times R_1$	$S_5 \times R_1$	$S_1 \times R_2$	$S_3 \times R_2$	$S_1 \times R_3$	$R_2 \times R_3$
[m]	0.33	8.68*	0.67*	7.72*	11.58*	4.58*
[d]	0.33	0.00	0.33	0.00	-6.92*	-4.58*
[h]	10.31*	-8.68*	16.73*	-6.95*	1.58	2.14
[i]	-8.68*			-7.72*		
[j]	10.64*	-6.65*	18.05*	9.27*	-4.06	-5.89
[l]	-10.64*		-17.39*		42.51*	-6.73
R^2	76.03	68.99	97.04	91.15	99.70	90.65

* Significant at p = 0.05

4.3.5 Glume colour

Family means: Means and standard errors of six families in the cross straw glume (S_5) × purple glume (R_1), for glume colour, are given in the Table 32. The means of P_1 and P_2 were significantly different, and the means of F_1 and F_2 tended towards the mid-parent value (3.5). On the other hand, BC_1 and BC_2 means tended towards the recurrent parent.

Frequency distributions: Frequency distributions of the families are depicted in Fig. 25. The F_2 showed bimodal distribution, while the F_1 was unimodal with an intermediate mode (score 4). Distributions of BC_1 and BC_2 overlapped with each other.

Generation mean analysis: Estimates of gene effects, in cross $S_5 \times R_1$ for glume colour are given in Table 32. The high R^2 value of 99.3% indicates that the model was a good fit. Additive gene action was the most important and significant effect observed for glume colour.

4.4 GENERATION MEAN ANALYSIS FOR GRAIN YIELD, AND YIELD COMPONENTS IN TWO SUSCEPTIBLE × RESISTANT CROSSES OF SORGHUM

Table 32. Means of different families and estimates of gene effects for glume colour in the cross $S_5 \times R_1$.

	P_1	P_2	F_1	BC_1	BC_2	F_2
Mean	1.00	7.00	3.93	2.53	5.33	3.87
SE	0.0	0.0	0.10	0.25	0.29	0.14

Estimates of gene effects			
[m]	[d]	[h]	[i]
3.89*	-3.00*	0.10	0.17

* Significant at p = 0.05

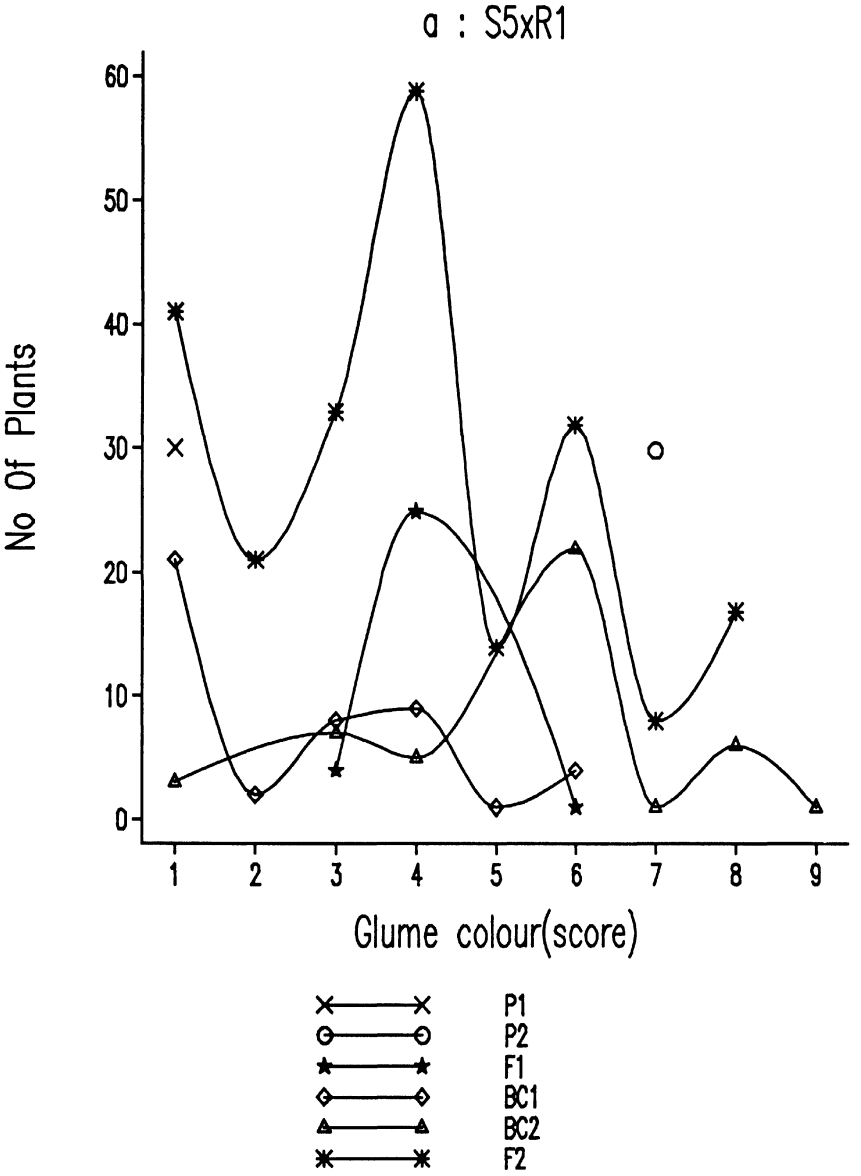


Figure 25. Frequency distributions of P_1, P_2, F_1, F_2, BC_1 and BC_2 families in a cross of sorghum for glume colour (1995).

4.4.1 Plant height

Family means: In two crosses, $S_1 \times R_1$ and $S_1 \times R_2$, F_1, BC_1, BC_2 and F_2 means tended towards the tall parent, (P_2), indicating dominance of tallness. In $S_1 \times R_1$, the F_1 mean was greater than that of the tall parent (Table 33).

Generation mean analysis: In both the crosses estimates of gene effects revealed significant additive effects. In $S_1 \times R_1$, dominance genetic effects and dominance × dominance interaction effects, were in the opposite directions and both were significant (Table 34). However in $S_1 \times R_2$, additive × dominance interaction was found most important.

4.4.2. Panicle length

Family means: In $S_1 \times R_1$, the F_1 mean was greater than those of both the parents, whereas in $S_1 \times R_2$, the F_1 mean tended towards P_2 (Table 33). Also, the BC_1 and BC_2 means tended towards P_2, while F_2 means tended towards the mid-parent value.

Generation mean analysis: In both the crosses, additive gene effects were important and significant. In $S_1 \times R_2$, both dominance × dominance gene interactions and additive × additive gene interactions were found significant (Table 34).

Table 33. Means of the families for grain yield and yield components in two crosses of sorghum.

Families	Plant height (cm)		Panicle length (cm)		Panicle weight (g)		Primary branches		Grain yield plant^{-1} (g)	
	S_1xR_1	S_1xR_2	S_1xR_1	S_1xR_2	S_1xR_1	S_1xR_2	S_1xR_1	S_1xR_2	S_1xR_1	S_1xR_2
P_1	160.0	156.0	26.0	27.5	47.5	41.3	46.9	43.5	28.0	28.9
P_2	301.2	296.0	31.0	30.4	43.3	50.3	35.0	48.2	27.6	36.2
F_1	312.5	292.0	33.0	29.5	94.8	79.0	47.9	52.2	64.9	55.2
BC_1	298.5	298.8	29.7	28.6	87.8	73.4	54.0	53.6	61.9	52.4
BC_2	318.3	289.2	31.6	29.3	74.4	70.0	55.6	54.3	47.5	50.2
F_2	275.2	289.2	29.1	28.2	46.1	43.3	51.8	48.1	28.4	26.9

Table 34. Estimates of the gene effects for grain yield and yield components in the two crosses of sorghum.

Cross	Plant height		Panicle length		Panicle weight		Primary branches		Grain yield plant^{-1}	
	$S_1 \times R_1$	$S_2 \times R_2$	$S_1 \times R_1$	$S_1 \times R_2$	$S_1 \times R_1$	$S_1 \times R_2$	$S_1 \times R_1$	$S_1 \times R_2$	$S_1 \times R_1$	$S_1 \times R_2$
[m]	227.0*	295.0*	28.5*	27.9*	42.8*	66.6*	31.1*	46.3*	76.0*	66.8*
[d]	-63.9*	-70.1*	-2.3*	-1.0*			4.9*			
[h]	171.7*					293.8*	66.2*	6.9*	276.6*	252.9*
[i]		-66.1*		1.5*		113.8*	9.9*		105.3*	97.9*
[j]		174.3								29.0*
[l]	-86.3*			1.7*	43.5*	148.3*	-49.3*		-135.7*	-130.9*
R^2	91.6	94.7	81.2	84.8	17.0	82.4	67.1	11.6	95.3	94.2

* Significant at p = 0.05

4.4.3 Panicle weight

Family means: In both the crosses, the F_1, BC_1 and BC_2 means were greater than those of both the parents. However, the F_2 mean tended towards the mid-parent value (Table 33).

Generation mean analysis: The R^2 value was very low (17%) in the cross $S_1 \times R_1$, while in $S_1 \times R_2$, the R^2 value was very high (82%). In $S_1 \times R_2$, dominance effects were most important (Table 34); dominance × dominance and additive × additive interactions, though significant, were of lesser magnitude. Further, the estimates of dominance and dominance × dominance interaction were in same direction (Table 34)

4.4.4 Primary branches

Family means: In both the crosses, the F_1, BC_1, and BC_2 means were greater than those of the parents (Table 33). In $S_1 \times R_1$, the F_2 mean was greater than those of both the parents but was less than those of BC_1 and BC_2. On the other hand, in $S_1 \times R_2$, the F_2 mean tended towards P_2 (R_2).

Generation mean analysis: In $S_1 \times R_1$ and $S_1 \times R_2$, R^2 values of 67.09% and 11.62%, respectively, were recorded. In $S_1 \times R_1$, dominance gene effects were found important; significant negative dominance × dominance gene interactions were also observed (Table 34).

4.4.5 Grain yield per plant

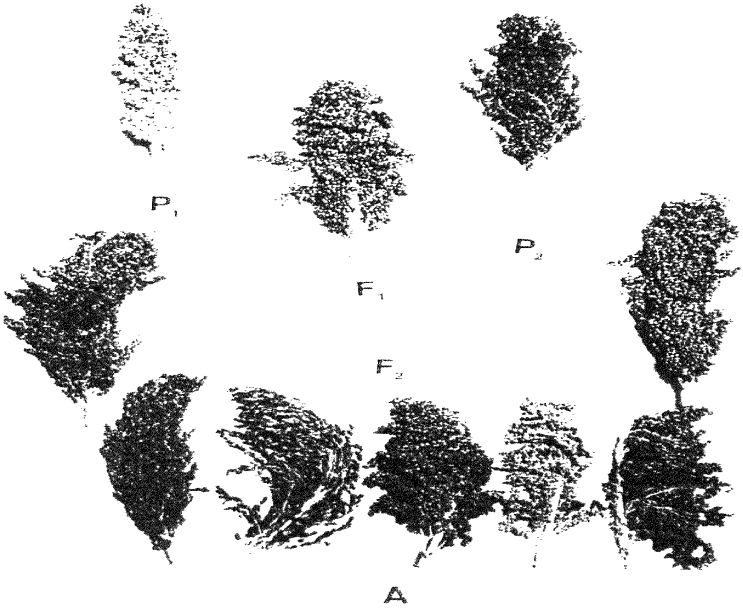
Family means: In both crosses, the F_1, BC_1, and BC_2 means were greater than those of parents. However, the F_2 mean values tended towards those of respective parents (Table 33).

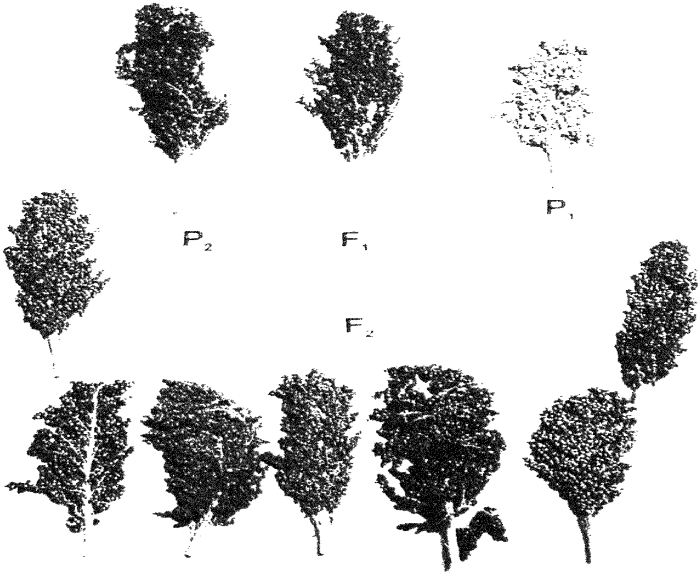
Generation mean analysis: Gene effects for grain yield per plant are given in the Table 34. In both the crosses, dominance and dominance × dominance effects were predominant. The values of both the estimates were high but were in the opposite directions. In these crosses, significant additive × additive gene effects were also observed.

In susceptible × resistant crosses, the F_2 and backcross generations showed large variability for disease reaction and agronomic characters (Plate 9). Two hundred and fifty progenies were advanced to F_4 and F_5 generations. About twenty progenies with good agronomic characters and moderate resistance to grain mould were selected for the breeding programme.

Plate 9. F_2 segregants in white susceptible x coloured resistant crosses.
A: MS 422B × IS 14387.
B: AKMS 14B × IS 14375.

Plate 9





Discussion

5 DISCUSSION

The potential yields of present day commercial hybrids are not fully realised as they are highly susceptible to grain moulds. Losses caused by grain moulds are both quantitative and qualitative (Esele, 1995). The changes in physical properties include decreased filling and size of the grain and a chalky endosperm which disintegrates during harvest and threshing, thus causing considerable loss in grain yields. The mouldy grain becomes unfit for human consumption leading to unremunerative price in the market causing losses to farmers. Most improved varieties and hybrids mature earlier than local varieties, often before the end of the rainy season. This results in increased exposure to grain moulds, greatly limiting the adoption of these improved varieties and hybrids (ICRISAT and FAO, 1996). Though the restorers of present day hybrids have good yield and some tolerance to pests and diseases, the male-sterile lines are medium to late, poor yielders and highly susceptible to grain moulds. Breeding grain mould resistant male-steriles and restorers is a prerequisite for planning an effective hybrid breeding programme aimed at durable resistance.

Breeding for biotic resistance can be taken up in the following stages.

(i) Locating the resistance gene(s) in the germplasm or defining the sources of such genes (Sharma, 1994).

(ii) Once the gene sources are detected and maintained, the next step is to identify the defence mechanisms (morphological and biochemical) operating in the resistance sources against pathogen(s) invasion (Sharma, 1994).

(iii) The third step is to identify the genetic control (gene action/inheritance) of resistance by simple crossing between two contrasting parents or by following some appropriate mating design, such as diallel. Segregation patterns in F_2, BC_1, and BC_2 generations can also define the nature and number of gene(s) involved in resistance (Sharma, 1994).

Exploitation of any genotype in a resistance breeding programme or for commercial release should ideally be preceded by knowledge about the number, nature and diversity of genes controlling resistance in the genotype. This information helps in deciding the breeding procedure to be followed to incorporate resistance into high yielding backgrounds. In the present study, several genotypes were evaluated for grain mould resistance, and certain morphological and biochemical characters associated with resistance. Resistant and susceptible genotypes were selected and crosses were made among them to study the genetics of grain mould resistance and other associated characters.

5.1 PERFORMANCE OF SORGHUM GENOTYPES FOR GRAIN MOULD RESISTANCE AND OTHER MORPHOLOGICAL CHARACTERS.

5.1.1 Means

Bandyopadhyay and Mughogho (1988) evaluated three techniques for mould screening and showed that mould resistance screening without inoculation and bagging of panicles was feasible if overhead sprinklers were used from flowering to harvest. In the present study, 22 sorghum genotypes, representing wide diversity, were screened under sprinkler irrigation for grain mould resistance and other traits. The means of these genotypes for different variables recorded are shown in Table 4.

Field grade score (FGS) and threshed grade score (TGS): The genotypes IS 14375, IS 14387, IS 18144, IS 18528, IS 24495, IS 25017, SP 33487 and B58586 were classified as mould resistant as they recorded low FGS and TGS values. These genotypes were also found to be resistant by others (Bandyopadhyay and Mughogho, 1988; Anonymous, 1995; ICRISAT, 1994). The genotypes 296B, SPV 475, SPV 462, MS 422B, AKMS 14B, AKR 150, were classified as susceptible as their mean FGS and TGS were high (score 4 to 5). Other reports (Anonymous, 1995) identified genotypes such as 296B, SPV 462 and SPV 475 as moderately resistant. One reason for these conflicting results could be the screening technique utilised in the studies. Screening techniques will be discussed in detail in 5.2.1 of this chapter. Castor and Frederiksen (1980) found that field ratings on natural or *Fusarium* inoculated heads would have permitted some susceptible sorghum lines

to escape detection as mould growth was hidden by the glumes and visible only after threshing. In the present study also some of the genotypes, *viz.*, SP 33487, GM 15373, and TNS 30 recorded moderate values for FGS, and high for TGS (Table 4). Genotypes such as SP 33316, SP 33349 and GM 15018 were classified as moderately resistant lines.

Grain germination: Earlier studies found that grain germination was so closely related to grain moulds that resistant genotypes could be identified from germination tests (Denis and Girard, 1977). In this study, the coloured seeded genotypes, which were identified as resistant sources (low FGS and TGS), showed high mean germination percentage. The susceptible genotypes, with high FGS and TGS, showed very low germination percentage. Similar results were observed by Mahalinga *et al.* (1988), Singh and Agarwal (1989), and Forbes *et al.* (1989). Some of the white-seeded lines showed good mean germination although they recorded moderate values for FGS and TGS. This indicated that the discoloration on the seed was superficial and very little damage had occurred internally. Castor and Frederiksen (1980) also observed similar results.

Ergosterol: Ergosterol is a steroid which is very much specific to fungi. The quantity of ergosterol in a grain sample is an index of fungal mass (Seitz *et al.*, 1977) and is another criterion for measuring grain mould damage. Table 4 shows the mean ergosterol content in the genotypes studied and Fig. 1 depicts

chromatographs indicating the different quantities of ergosterol in susceptible and resistant genotypes. Forbes *et al.* (1989) and Jambunathan *et al.* (1991) reported that concentration of ergosterol was 10-fold higher in susceptible than in resistant genotypes. In the present study, genotypes such as 296B, SPV 462, SPV 475, AKR 150, MS 422B and AKMS 14B recorded high mean ergosterol content confirming the results observed from FGS, TGS and germination studies. On the other hand, genotypes IS 14375, IS 14387, IS 18144, IS 18528, IS 24495, IS 25017, B58586 . and IS 21443 recorded low mean ergosterol content confirming their resistance to grain moulds.

Glume phenols: Morphological characters such as panicle shape, glume and seed size and colour and days to flower play an important role in governing mould resistance. The glume appears to be the plant's first defence mechanism against grain moulds (Waniska *et al.*, 1992). Phenolic compounds in the glume increased 20 d after anthesis, especially in resistant and moderately resistant cultivars (Mansuetus *et al.*, 1988; Waniska *et al.*, 1992). In this study also, resistant and moderately resistant lines IS 14387, IS 14375, IS 18144, IS 18528, SP 33349, SP 33316 (white seeded) and GM 15018 (white seeded), recorded high content of glume phenols in both methanol extracts and acid-methanol extracts 30 d after anthesis. On the other hand, white seeded resistant genotypes, *viz.*, B58586 and IS 21443, recorded very much lower content of glume phenols in the glumes comparable to that recorded in susceptible genotypes such as 296B and SPV 475.

The line SP 333487 recorded very high phenol content in glume, showed moderate FGS and high TGS score. From this study it appears that content of phenols in the glumes is one of the important characters governing grain mould resistance.

Seed phenols: Brown coloured seed, with testa having high phenolic acid content was the most influential seed characteristic affecting mould resistance in several studies (Ellis, 1972; Hahn *et al.*, 1983; Hahn and Rooney, 1985; Jimenez and Vallejo, 1986; Esele *et al.*, 1993). Menkir *et al.* (1996a) found that resistance to grain mould was not always related to a high concentration of tannin in brown sorghums. They further reported that higher levels of resistance to moulding seem to arise from the combined effects of tannin and flavan-4-ols. In the present study, the lines with high content of phenols in the seed were IS 14375, IS 14387, IS 18144, IS 18528 and SP 33487; except for the line SP 33487, all other lines were found resistant to grain moulds.

Glume flavan-4-ols: Flavan-4-ols in glumes are not reported in the literature. In the present study, flavan-4-ols were detected in the glumes 30 d after anthesis in coloured seed lines IS 14375, IS 18144, IS 18528, SP 33349, and white seed line SP 33316. It is interesting to note that white seed line SP 33316, with moderate FGS and TGS, showed moderate resistance to grain moulds.

Seed flavan-4-ols: Grain mould resistance has been found to correlate strongly with high concentration of flavan-4-ols in seeds (Butler, 1982; Jambunathan *et al.*, 1991; Martinez *et al.*,1994). All the lines with flavan-4-ols in glumes, except white seeded SP 33316, recorded high flavan-4-ols in seeds also 30 d after anthesis.

Seed hardness: Sorghum kernels with more corneous endosperm and hard seed were more resistant to grain moulds than those with floury endosperm (Ibrahim *et al.*, 1985; Jambunathan *et al.*, 1992; Mukuru, 1992; Kumari and Chandrashekar, 1992). However, Menkir *et al.* (1996a) found that resistance was not always associated with corneous endosperm in white sorghums. In the present study the resistant sources IS 14375, IS 14387, IS 18528, and SP 33349 with coloured seed, and IS 24495, IS 25017, B58586 and IS 21443 with white seed, were relatively hard seeded and were moderately resistant. However, white seeded lines recorded only moderate hardness. Susceptible lines 296B, SPV 462, SPV 475 and MS 422B were very soft seeded. One coloured resistant line, IS 18144, recorded moderate hardness of seed.

Days to flower: The genotypes showed large variation for flowering. The studies did not show any clear pattern; both susceptible and resistant genotypes were early, medium and late flowering. Similar results were observed by Ibrahim *et al.* (1985), Mukuru (1988), and Menkir *et al.* (1996b).

Plant height and grain yield: In general, the resistant lines were taller and the susceptible lines were higher grain yielding.

Glume cover: Seeds completely enclosed in long papery glumes were found to show resistance to grain moulds (Murty, 1977). However, Williams and Rao (1980) concluded that there was no apparent correlation between resistance and grain glume cover. In this study also only three resistant lines, IS 21443, IS 18144 and IS 18528, showed maximum glume cover on the seed.

Glume colour: All the coloured resistant lines recorded dark coloured glumes. Some of the white resistant and moderately resistant lines, *viz.*, for example IS 25017, GM 15373, SP 33316 and GM 15018, also had coloured glumes. Mansuetus *et al.* (1988) found that darker glume colour had increased phenolic acid and was related to resistance.

Seed colour: All the lines with coloured seeds, except SP 33487, were found grain mould resistant. Similar results were observed by Jambunathan *et al.* (1986). SP 33487, which recorded high quantity of phenols in its glume and seed, was susceptible to grain mould presumably because of its soft grain texture.

Glume index: The genotypes showed large variation for glume index and the trait did not show clear relationship to grain mould resistance.

5.1.2 Correlations

Correlations between different morphological characters: Correlations between 17 characters, recorded on the 22 genotypes are given in Table 5. Field grade score (FGS) showed strong positive correlations with threshed grade score (TGS). Williams and Rao (1981) reported that FGS could be misleading because some cultivars developed mould on the rachis and glume but maintained clean seed, and vice versa.

Ergosterol concentration serves as an index of grain mould infection. In the present study, FGS showed strong positive correlations with ergosterol content. Forbes *et al.* (1989) and Jambunathan *et al.* (1991) reported that the quantity of ergosterol was highly correlated to visual grain mould.

Seed germination was adversely affected by grain moulds; seed viability and germination decreased with increasing infection by mould causing fungi (Mahalinga *et al.*, 1988; Singh and Agarwal, 1989; Forbes *et al.*, 1989). In the present study also, FGS showed strong negative correlation with germination percentage.

Among genotypes studied, FGS showed high negative correlation with seed hardness, and from the mean data it is clear that the resistant lines with coloured seed were also hard seeded. In white seed lines, resistance was ascribed to seed

hardness (Jambunathan *et al.*, 1992). However, in brown sorghum, increased levels of resistance to grain mould were not associated with endosperm texture (Menkir *et al.*, 1996a).

FGS showed significant negative correlations with glume colour, phenols in acid-methanol extracts of glumes and with flavan-4-ols in glumes (Table 5). Glume colour in turn showed significant positive correlations with phenols and flavan-4-ols in glumes and seeds.

FGS showed significant positive correlation with grain yield/ plant indicating that the susceptible lines studied were higher yielding. On the other hand, FGS showed significant negative correlation with seed phenols. Harris and Burns (1973), Doherty *et al.* (1987) and Menkir *et al.* (1996a) reported strong association between phenols and mould resistance.

Grain mould score showed significant negative correlations with glume cover, glume length and glume area when the cultivars were inoculated, and correlations were nonsignificant when the cultivars were not inoculated (Mansuetus, 1990). In the present study also FGS revealed significant negative correlation with glume cover.

Three other grain mould measuring variables, *viz.*, threshed grade score, percentage seed germination and ergosterol, showed correlations similar to that of FGS. TGS, ergosterol content and percentage germination showed strong negative correlations with seed hardness, glume colour, seed phenols and flavan-4-ols.

Intragroup correlations: Grouping of 22 genotypes based on seed colour, glume colour and seed hardness, and correlations of these characters with FGS and TGS within each group are given in Tables 6, 7 and 8. In the coloured seed, coloured glume and soft seed groups, FGS and TGS showed substantial negative correlations with glume colour. Likewise, FGS and TGS also showed significant negative correlations with seed hardness in the white seed, straw glume, coloured glume, soft seed and hard seed groups.

Correlations in the F_2 generation: Table 9 shows the correlation matrix for the characters observed in the F_2 of cross between straw glume line (S_s) and purple glume line (R_1). These results also confirmed the strong negative correlations of FGS and TGS with glume colour. Figs 2 and 3 depict that the FGS and TGS values decreased as the glume colour increased in P_2, BC_2 and F_1 families. The strong correlation between mould resistance and glume colour, in different generations, could also be due to linkage between the characters. From these results it is apparent that glume colour/phenols and flavan-4-ols are important characters

contributing to grain moulds resistance in the genotypes studied. Mansuetus (1990) also reported similar results.

An overview of the means and correlations indicates that seed hardness, glume colour, seed phenols, seed flavan-4-ols and glume cover, in association with one another, bring about high resistance to grain moulds. Menkir *et al.* (1996a) reported that, even among brown sorghum accessions, higher levels of resistance to moulding seemed to arise from the combined effect of tannin and flavan-4-ols. The tannins in brown sorghums are polyphenols, which render the grain astringent and unpalatable. High tannin levels result in low digestibility and reduced protein efficiency ratio and thus present problems of utilisation of brown coloured seed (Butler, 1982). Glumes with intense red and purple colour have a tendency to stain the sorghum kernels in humid conditions (Rooney and Miller, 1982). Threshing is difficult in sorghum lines with long enclosed glumes; in guinea sorghums, glumes cover the seed up to physiological maturity and open up only at the time of harvest. Very hard seeds have low digestibility and are not suitable for some food preparations. Hence it is important to strike a balance between the level of grain mould resistance and grain hardness. Thus breeding for light glume colour with high levels of glume flavan-4-ols, moderate seed hardness, glume cover up to 30 d after anthesis along with free threshing might result in mould resistant lines with desirable grain quality.

5.2 GENERATION MEAN ANALYSIS FOR GRAIN MOULD RESISTANCE IN DIFFERENT CROSSES OF SORGHUM.

Susceptible and resistant genotypes were selected for study of the genetic basis of resistance after evaluating sorghum genotypes for grain mould resistance and characters associated with resistance. The genotypes selected for crossing and their ancillary data are given in Table 3. Ten and eight resistant × susceptible crosses were analysed for grain mould resistance under sprinkler irrigation during 1995 and 1996, respectively. Though the values were different for field grade score and threshed grade score, the trends were very similar and hence they were treated together as measures of resistance to grain moulds.

5.2.1 Field grade score and threshed grade score

Family means: Mean values of the parents, F_1, F_2, and backcross generations for FGS and TGS during 1995 and 1996 are given in Tables 10, 11, 15 and 16. The genotypes S_1, S_5 and S_6 were consistently susceptible, while R_1 and R_2 were found resistant over the years. However, genotypes S_2, S_3 and R_{16} were moderately resistant during 1994, while S_2 and S_3 were rated susceptible during 1995 and R_{16} during 1996. Similarly, R_3, a white resistant genotype, was scored as resistant during 1994, susceptible during 1995 and moderately resistant during 1996. Bandyopadhyay and Mughogho (1988) reported that when ambient humidity is low,

sprinkler irrigation may be ineffective in maintaining sufficient humidity for grain mould development. Fig. 26 depicts rainfall distribution during the crop growing period of three years from 1994 to 1996. High rainfall was recorded during weeks 9 to 11 of 1994, during weeks 10 to 13 of 1995 and during weeks 3 to 6 of 1996. Forbes *et al.* (1992) reported that post-maturity colonisation is generally what produces the mouldy appearance of grain maturing in humid environments. Heavy rains at grain maturity, especially during the critical period from 30 to 50 d after anthesis, cause maximum grain damage (Castor and Frederiksen, 1980). Figures 27 and 28 illustrate the rainfall patterns of 1995 and 1996 during the post-maturity periods of different genotypes. The post-maturity period, i.e., 30 to 50 d after anthesis, of IS 25017 R_3, white resistant source, coincided with heavy rainfall weeks during 1995 and low rainfall weeks during 1996. Accordingly, the mean FGS of R_3 was high during 1995 and moderate during 1996. It appears that the white resistant sources are rather unstable and the FGS reaction of such genotypes depends on the level of ambient humidity during the post-maturity period. Bandyopadhyay and Mughogho (1988), in their screening experiments under inoculation and bagging, observed that only one genotype IS 14332 behaved differently during 1983 (FGS 2.6 to 2.9) and 1984 (FGS 3.2 to 3.4). Incidentally IS 14332 is also a white resistant source. Though the sprinkler irrigation screening technique is efficient, there is a need for developing a superior technique to avoid inconsistent results while evaluating white resistant sources.

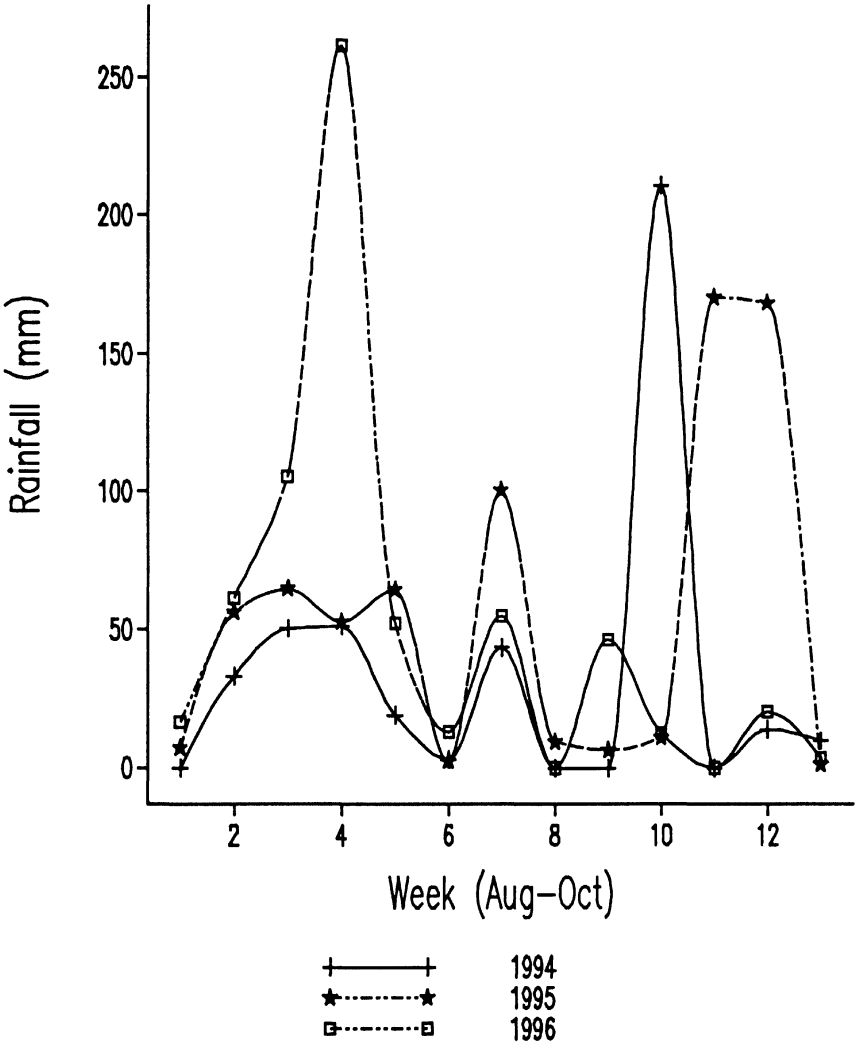


Figure 26. **Rainfall distribution during three years (1994-1996).**

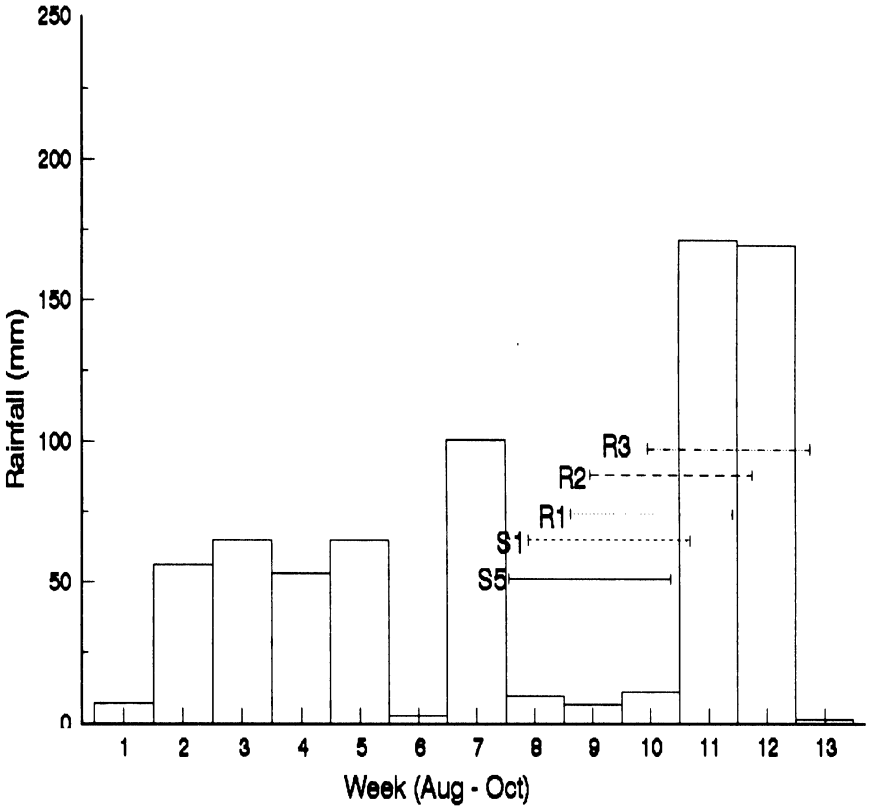


Fig. 27. Post-maturity period of sorghum genotypes and rainfall pattern during 1995.

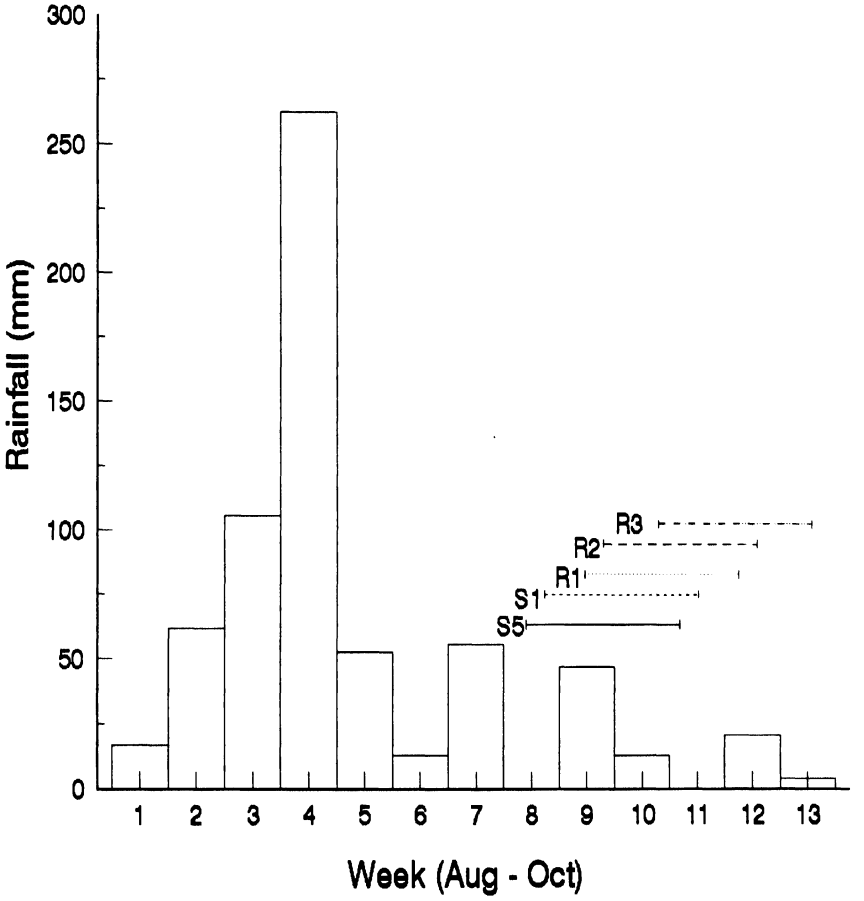


Fig. 28. Post-maturity period of sorghum genotypes and rainfall pattern during 1996.

The family means of different crosses grown during 1995 and 1996, for FGS and TGS are given in Tables 10, 11, 15 and 16. In $S_1 \times R_1$, $S_2 \times R_1$, $S_5 \times R_1$, $S_6 \times R_1$, $S_1 \times R_2$, $S_2 \times R_2$ and $S_3 \times R_2$ crosses, F_1 means tended towards the resistant parent, indicating that resistance is governed by dominant genes. The F_2 means, in general, also tended towards the resistant parent , confirming dominance of resistance genes.

In the white susceptible (S_1) × white resistant (R_3) cross, the F_1 mean value was equal to the midparent value during 1995 and tended towards the resistant parent, during 1996. These differences are attributed to the varied behaviour of resistant parent (R_3) during 1995 and 1996. Also the mean values of the F_1 in $R_2 \times R_3$ cross were found different during 1995 and 1996. The F_2 mean value tended towards the resistant parent, (R_2), during 1995 while it tended towards moderately resistant parent (R_3) during 1996. This may be attributed to the inconsistent behaviour of R_3 for FGS during these years.

Both the parents of $S_1 \times R_6$ and $S_1 \times R_{16}$ crosses scored high FGS and the F_1 mean values were less than that of both parents indicating that the parents may have modifier genes for high susceptibility. However, in a resistant (R_1) × resistant (R_2) cross, the FGS means of the parents were low and showed nonsignificant differences; however, the F_1 mean showed higher value than that of both parents, presumably because of nonallelic major genes besides minor modifiers contributed by the parents.

The inconsistent inheritance pattern observed over years in different crosses may be attributed to the diverse resistance genes that specify different mechanisms of resistance to grain mould.

Frequency distributions: The F_2 distributions in most of the crosses, in general, were bimodal or unimodal with modes in the 2 to 4 range and an extended tail towards higher scores with minor peaks indicating a second mode (Figs 4 to 13). These distributions reveal that grain mould resistance is determined by both major and minor genes. The distributions of F_1 and F_2 were skewed towards the resistant parent, suggesting that mould resistance is governed by dominant genes; and the distributions of BC_1 and BC_2 in most of the crosses, imply epistatic interactions between genes. Crosses $S_3 \times R_2$ and $R_2 \times R_3$ showed a second mode in the range of 6 to 8, which was more frequent than the first mode observed at 2 to 4, suggesting more than two genes for resistance. The F_2 distribution, $R_1 \times R_2$ cross, showed some susceptible segregants with a FGS of 5 to 8, indicating different resistance genes in R_1 and R_2. In the F_2 generation of two crosses, $S_1 \times R_{16}$ and $S_1 \times R_6$, tested during 1996, a few segregants with lesser FGS values than the resistant parents were observed, indicating transgressive segregation for increased mould resistance caused by modifier genes. Inconsistent frequency distributions in different crosses for FGS and TGS over two years suggest that a number of major genes in conjunction with minor modifiers determine grain mould resistance.

Segregation pattern: Since most of the frequency distributions in different crosses showed strong peaks at FGS 4, plants showing FGS values of 1 to 4 (1 to 15% seed with mould) were classified as resistant and remaining plants with FGS of 5 to 9 were classified as susceptible. Segregation pattern for FGS and TGS calculated on this basis are given in Tables 12 and 17. Segregation patterns in F_2, BC_1 and BC_2 for FGS of different crosses are described below.

1. White susceptible × red resistant (R_1) crosses: In $S_1 \times R_1$, $S_5 \times R_1$ and $S_6 \times R_1$ the F_1 hybrids were resistant and red in colour. The F_2 segregation ratios of 9 resistant(R) : 7 susceptible(S) and 1R:3S ratios observed in BC_1 indicate duplicate recessive epistasis. Obviously, two independently assorting dominant genes are complementing with each other in determining resistance. Similar results were reported by Esele *et al.* (1993) in a cross between red resistant and white susceptible parents; they suggested interaction between a pericarp gene and an intensifier gene for grain mould resistance. These results amply indicate that grain mould resistance in the red resistant (R_1) line is governed by two nonallelic genes.

In one of the white susceptible (S_2) × red resistant (R_1) crosses, a F_2 segregation ratio of 51R:13S and BC_1 ratio of 1R:1S were observed, suggesting interaction among three nonallelic dominant genes. Apparently, the resistant parent (R_1) has two major dominant genes that act in an additive fashion in determining grain mould resistance, while the susceptible parent (S_2) contributes a dominant epistatic gene

that inhibits the expression of only one of the two dominant genes of the resistant parent.

2. White susceptible × brown resistant (R_2) crosses: These crosses showed modified trigenic ratios with varied gene interactions (Tables 12 and 17). In $S_1 \times R_2$, the F_2 segregation fitted to 39R:25S ratio, indicating interaction among three nonallelic gene pairs-one basic, one inhibitory and one anti-inhibitory in action. Further BC_1 ratio of 1R:3S suggests that the dominant inhibitory gene is contributed by the susceptible (S_1) parent.

In $S_2 \times R_2$, the F_1 was resistant and the F_2 segregation fitted 45R:19S ratio, implying interaction among three nonallelic genes. In this cross, the combined action of a basic dominant gene with two duplicate complementary genes seem to determine grain mould resistance. Also, the BC_1 segregation ratio of 1R:1S suggests that one of the dominant duplicate genes is contributed by the susceptible (S_2) parent.

3. Brown resistant (R_2) × white resistant (R_3) and white susceptible (S_3) × brown resistant (R_2) crosses: The observed F_2 segregations fitted to the modified trigenic ratio of 27R:37S implicating three nonallelic major genes acting in a complementary fashion. In these crosses, the F_1s were resistant, and the backcrosses generations segregated into 1R:7S ratio. Esele *et al.* (1993) reported similar results for F_2 segregation in a brown resistant × white susceptible cross.

4. Red resistant (R_1) × brown resistant (R_2) cross: The F_2 segregation in this cross fitted to the modified trigenic ratio of 57R:7S indicating complex interaction among three nonallelic genes. Apparently, a basic dominant gene for resistance and a pair of complementary genes are involved in the inheritance of mould resistance. The observed BC_1 segregation of 3R:1S suggests that one of the dominant genes is contributed by the red parent (R_1). According to Esele *et al.* (1993), the genes which governed resistance in a red resistant source were pericarp colour genes and the intensifier genes; and in the brown resistant lines, it was pericarp genes and testa genes that governed resistance. In such cases, red × brown crosses should give monogenic or digenic ratios since the two parents differ in one or two testa genes. However, in the present study, a trigenic ratio was observed beside recovery of some susceptible plants, indicating that the two parents differed not only in testa genes but also for some other gene(s).

From these segregation patterns of modified dihybrid and trihybrid ratios, observed in different crosses, it may be concluded that diverse nonallelic dominant genes are governing grain mould resistance. One to two basic dominant genes from the resistant parent and one dominant gene contributed by the susceptible parent might interact to produce mould resistance. The dominant gene from the susceptible may be different in different susceptibles or is modified to behave differently in different parents. Similar results were reported by Shivanna *et al.* (1994); in a coloured resistant × white susceptible cross, it was observed that resistance was governed by

four genes, two genes with complementary interaction and the other two with additive effects. They further reported that resistance was due to four alleles, interacting additively, at two loci. Also, the resistant parent contained one of the dominant complementary genes, while the susceptible parent contributed the other dominant complementary gene.

Generation mean analysis: Generation mean analysis was conducted on a set of transformed square root data. Although this transformation produced a change in the scale of the observations, it did not seem to affect the interpretation of the data. Estimates of genetic effects on the original scale were comparable with those produced on the transformed scale.

Estimates of genetic effects for FGS and TGS are given in Tables 13, 14, 18 and 19. For both the variables, in general, similar results were obtained. Though the R^2 values obtained were very high (up to 99%), the χ^2 values in some crosses were high indicating that the model was not a good fit. Similar results were reported by Torres *et al.* (1993); they chose regression analysis method as the most adequate test for generations derived from common parents; and discarded the χ^2 proposed by Mather and Jinks (1971) as the addition of F_2, F_3 etc. mean values inflates the χ^2 value.

The R^2 values obtained in all the crosses were very high (84 to 100%) indicating that the model was a good fit for FGS and TGS during 1995 and 1996. In both the years additive genetic effects were significant. Though the means of F_1 and F_2, frequency distributions and segregation patterns revealed dominance effect to be the most important, yet the estimates showed significant additive gene action in all the crosses. Some of the genes may have similar but contrasting dominance effects which cancel each other (Mansur, 1993). Nelson (1984) observed the expression of additive gene effects by a number of dominant genes when put together. Esele *et al.* (1993) reported that genes which conferred dominant grain mould resistance individually showed additive effects when present together.

Additive effects were significant in all the crosses except $R_1 \times R_2$, during 1995 and 1996. Negative dominance effects were found significant in five crosses and were of greater magnitude in $S_1 \times R_2$, $S_3 \times R_2$ and $S_5 \times R_1$ during 1995, and in $S_1 \times R_1$ and $S_1 \times R_{16}$ during 1996. Significant negative dominance x dominance interactions were present where dominance effects were absent during 1995. Also significant negative additive x dominance interactions were found in greater magnitude in $S_1 \times R_1$, $S_1 \times R_2$, $S_5 \times R_1$ and $R_2 \times R_3$ during 1996. Further additive x additive interactions were found significant in three and seven crosses during 1995 and 1996, respectively. Murty and House (1984) and Kataria *et al.* (1990) reported large dominance effects besides significant additive effects and additive x additive interaction effects for grain mould resistance. In other studies, additive gene action was predominant in the

inheritance of resistance (Narayana and Prasad, 1983) and both additive and non-additive components of variance determined the expression of mould reaction (Dabholkar and Baghel, 1983).

Additive and dominance estimates were of higher magnitude during 1995 and 1996. However, negative additive × dominance interactions were of higher magnitude in some of the crosses during 1996. In two white susceptible × white resistant crosses, $S_1 \times R_3$, and $S_1 \times R_6$ additive and additive × additive interactions effects were important components of inheritance. A simple recurrent selection or a backcrossing scheme should work quite well to concentrate the frequency of resistance genes.

As the F_1 was more resistant than both parents in a white susceptible × white resistant cross, for FGS, a resistant hybrid can be developed from moderately resistant male sterile and restorer lines. In white susceptible × red resistant or in white susceptible × brown resistant, additive gene effects were predominant but dominance effects were also observed. Although fixable additive gene effects are present in almost all the crosses, the presence of dominance and complementary epistasis would tend to retard the progress through selection in early generations. Thus selection for grain mould resistance would be more effective if dominance and epistasis effects were reduced after a few generations of selfing.

Genotype x Environment (GxE) interactions: Although consistent additive gene effects were observed in all crosses during 1995 and 1996, dominance and other interactions were also observed during two years (Tables 13, 14, 18 and 19). Estimates of genotype (G) x environment (E) interactions from pooled data of 1995 and 1996 in six different crosses for FGS and TGS, are given in Tables 20 and 21. In GxE studies, important additive and dominance gene effects of equal magnitude were observed. In $R_1 \times R_2$, $S_1 \times R_3$ and $R_2 \times R_3$ environmental effects were significant but were of lesser magnitude. Also, in $R_2 \times R_3$, $R_1 \times R_2$ and $S_1 \times R_3$ environment x dominance (exh) interactions were found significant.

From the overall results of family means, frequency distributions, segregation pattern and generation mean analysis, it may be concluded that grain mould resistance is determined by various major genes which are modulated by several minor modifiers. In general, additive and dominance gene actions were found predominant. Environment and environment x dominance interactions, though of lesser magnitude, nevertheless influenced various crosses involving IS 25017, a white resistant line (R_3) as one of the parents.

5.3 GENETICS OF RELATED MORPHOLOGICAL CHARACTERS IN DIFFERENT CROSSES OF SORGHUM

5.3.1 Days to flowering

Most improved varieties/hybrids mature earlier than local varieties, resulting in increased grain mould susceptibility. Although, low correlations were observed between grain moulds and flowering in the present and earlier studies, there is a need to develop early-maturing grain mould resistant male-sterile and restorer lines for breeding higher yielding resistant hybrids.

Family means: Means of various families in the crosses for days to flowering tested during 1995 and 1996, are given in the Tables 22 and 23. In all crosses except in $S_5 \times R_1$ and $S_1 \times R_3$ the F_1 mean tended towards the early parent. Also the mean value of BC_1 and F_2 tended towards the early parent indicating that earliness is governed by dominant gene.

In two crosses, $S_1 \times R_3$ and $S_5 \times R_1$, the F_1 mean was close to the midparent value. The means of BC_1 and F_2 were less than that of F_1 mean and tended towards the early parent in $S_1 \times R_3$. These results indicate additive gene action in these two crosses. Similar results were observed for $S_1 \times R_1$, $S_1 \times R_2$, $S_1 \times R_3$ and $R_1 \times R_2$ grown during 1995 and 1996. The F_1 mean was closer to the midparent value during 1995 and to the late parent during 1996. The mean values of the two parents in cross $S_1 \times R_6$ were not different while the F_1 mean tended towards the late parent.

Frequency distributions: F_2 frequency distributions revealed bimodal to pentamodal distributions (Figs 14 to 18) indicating the involvement of more than two major genes in the inheritance of days to 50% flowering. In all the crosses, except in $S_5 \times R_1$ and $S_1 \times R_3$ the distributions of F_1 and BC_1 overlapped with that of the early parent grown during 1995. The frequency distributions in these crosses amply indicate the dominance of earliness. In $S_5 \times R_1$ and $S_1 \times R_3$, the F_1 distribution tallied with the midparent value. Transgressive segregants for earliness were observed in $S_1 \times R_2$, $S_2 \times R_1$, $S_6 \times R_1$, $S_1 \times R_2$, $S_2 \times R_2$ and $S_1 \times R_3$, indicating that different sets of genes were controlling this character. In general, the study shows that the character is governed by more than two major genes and that there is dominance for earliness in F_1 hybrids.

Generation mean analysis: R^2 values obtained during 1995 and 1996 were very high indicating that the model was a good fit (Tables 24 and 25). However in crosses, $R_1 \times R_2$ and $S_3 \times R_2$, R^2 values were very low indicating inadequacy of the model. During 1995 and 1996, additive gene effects were found to be of prime importance. Similar results were reported by Kirby and Atkin (1968), Harer and Bapat (1982), Deshmukh (1983), Kukadia *et al.* (1983), Chandrashekharappa (1987), Mallick and Gupta (1988) and Senthil and Palanasamy (1994). However, in one cross $R_1 \times R_2$, dominant gene action was more important during 1996. Whereas, eight and two crosses showed significant additive × additive gene interactions grown

during 1995 and 1996, respectively. Likewise, in five crosses, positive additive × dominance estimates were found to be important and contributed to lateness.

Although, additive gene action and its first order interaction are fixable, epistatic gene effects cannot be utilised as they operate in opposing directions. It may be necessary for selection pressure for duration to be lenient in early selfed generations and intensified when homozygosity is approached. Breeding procedures to be followed for grain mould resistance and earliness seem to be the same in susceptible × resistant crosses.

5.3.2 Seed colour

Several authors have reported the importance of seed colour/seed phenols in governing resistance to grain mould. In the present study also susceptibility to grain moulds showed negative correlation with seed colour.

Family means: Family means for seed colour in various crosses are given in the Table 26. In white × red crosses, the mean values of F_1, BC_2 and F_2 were greater than that of P_2 (red parent) indicating red to be dominant. In white × brown crosses, the F_1, BC_2 and F_2 mean values tended towards the brown parent indicating brown colour to be dominant.

Frequency distributions: Frequency distribution studies (Figs 19-21) showed a similar trend to that of family means. In various crosses, the F_2 distributions showed 2-3 peaks giving an impression of bimodal distributions indicating that seed colour is governed by two genes. In white × red cross and in red × brown crosses the F_2 distributions showed a peak at score 5 (red colour). In brown × white crosses, the F_1 distributions overlapped with that of P_2 showing brown to be dominant. Similar results were reported by Stephens (1946), Quinby and Martin (1954), and Rooney and Miller (1982).

Generation mean analysis: In various crosses, R^2 values obtained for seed colour were very high indicating the adequacy of the model tested. In most of the crosses, except in $S_1 \times R_2$, the dominant gene action was found significant and of greater magnitude. However, in a few crosses, additive gene action was important. Out of the three interactions, (complementary) dominant × dominant interactions were found most important. These results indicate that a resistant coloured hybrid is easy to produce.

5.3.3 Glume cover

The present study indicated the importance of glume cover in grain mould resistance. Knowledge of its inheritance pattern would help in breeding resistant lines.

Family means: The mean values of parents in crosses $S_1 \times R_1$, $S_1 \times R_2$ and $R_1 \times R_2$ were not different (Table 28). In most of the crosses the mean value of F_1 and F_2 were greater than the mean value of both parents showing overdominance for this character. In the cross $S_1 \times R_3$, the F_1 mean tended towards the larger parent showing dominance to be important in this cross.

Frequency distributions: In crosses, $S_1 \times R_1$, $S_2 \times R_1$ and $S_6 \times R_1$, the F_2 distributions were bimodal (Figs 22-24), implying involvement of two genes for this character. On the other hand, in seven crosses F_2 distributions showed normal symmetrical distributions indicating polygenic nature of the character in these crosses. Singh (1987) reported that the open and closed glume character expression indicated its dominance and recessiveness, respectively. Kullaiswamy and Goud (1982) found that three pairs of genes were involved for gaping glumes and gaping glumes were dominant over normal glumes. However, Khusnetdinova and El'konin (1989) found that long glumes were dominant to short glumes and further reported that different number of genes controlled the character in different genotypes.

Generation mean analysis: In all crosses, except in $S_1 \times R_3$, R^2 values were very high, indicating the model to be a good fit (Table 29). However, in $S_1 \times R_3$, low R^2 value was obtained indicating the presence of higher order interactions or environmental interactions. In various crosses, additive gene action was found but dominance gene action was more important and of higher magnitude. Also,

dominance × dominance and additive × dominance interactions were important. However dominance and dominance × dominance effects were in opposite directions showing duplicate epistasis.

The dominance effects may be utilised in hybrid breeding programme or selection pressure can be lenient in early selfed generations and intensified later when homozygosity is approached.

5.3.4 Preharvest sprouting

Preharvest sprouting leads to reduced seed viability and enhances the development of grain moulds (Castor and Frederiksen, 1977). Resistance to preharvest sprouting may also result in resistance to grain moulds.

Family means: In all six families, sprouting was noted only in $S_1 \times R_3$ (Table 30). The means of the F_1 and BC_2 were greater than the P_2 and F_2 and BC_1 mean was towards P_2 showing overdominance for this character.

Generation mean analysis: While in all crosses, except in cross $S_1 \times R_3$ dominance interaction was important; additive × dominance interaction was significant. Out of four crosses, two showed negative dominance effects. The results were inconsistent and interpretations were difficult (Table 31).

5.3.5 Glume colour

In the present study glume colour was observed to be one of the most important characters to be associated with grain moulds. The inheritance pattern of this character could be useful in a resistance breeding programme.

Family means: The means of F_1 and F_2 in the cross studied ($S_5 \times R_1$), tended towards the midparent value (Table 32). BC_1 and BC_2 means tended towards their recurrent parent indicating additive gene action.

Frequency distributions: Bimodal distributions with four peaks were observed in F_2 distributions showing involvement of more than two genes (Fig. 25). F_1 distribution was intermediate indicating additive nature of glume colour. Shivanna and Patil (1988), found digenic interactions while crossing black-glumed with straw-glumed lines, and Jayaramaiah and Goud (1982) reported trigenic ratios for this character. On other hand, Mani (1986) and Rao and Rana (1989) found monogenic inheritance and reddish-purple glume to be dominant over blackish-purple glumes.

Generation mean analysis: R^2 value obtained in the cross $S_5 \times R_1$ was very high showing the model to be a good fit (Table 32). Significant additive gene action was the most important. Dominant and additive × additive interactions were

nonsignificant. Simple recurrent selection should work quite well to achieve desirable glume colour.

High grain mould resistance can be incorporated into coloured hybrids by a judicious manipulation of seed colour and glume cover genes in hybrid breeding programmes. To get improved inbred lines for resistance is difficult and time consuming, due to the presence of dominance and epistatis for resistance to grain moulds as well as for the characters associated with resistance. It may be necessary for selection pressure to be lenient in earlier selfed generations and intensified later when homozygosity is approached.

5. 4 GENERATION MEAN ANALYSIS FOR GRAIN YIELD AND YIELD COMPONENTS IN SUSCEPTIBLE × RESISTANT CROSSES OF SORGHUM.

A better understanding of the inheritance pattern and magnitude of various types of gene action governing different agronomic traits can help in achieving high yielding grain mould resistant genotypes. Hence the present study investigated the genetics of grain yield and yield components in two susceptible × resistant crosses.

5.4.1 Plant height

Family means and generation mean analysis: The means of F_1, BC_2 and F_2 tended towards the higher parent, P_2 showing dominance for tallness (Table 33). Plant height is governed by four genes (Quinby and Martin, 1954). Generation mean analysis studies showed significant additive gene effects were common in both crosses (Table 34). In cross $S_1 \times R_1$, dominance and dominance × dominance interactions were more important. Similar results were reported by Kulkarni and Shinde (1987), Nimbalkar and Bapat (1987), and Mallick and Gupta (1988). On the contrary Harer and Bapat (1982), Deshmukh (1983) , Palanisamy and Subramanian (1986), Chandrashekharappa (1987), Yang (1991) and Senthil and Palanasamy (1994) reported that only additive gene action was important.

5.4.2 Panicle length

Family means and generation mean analysis: Mean value of F_1 tended towards the larger parent in cross $S_1 \times R_1$, while the mean value of F_1 in $S_1 \times R_2$, was greater than both the parents (Table 33). The results indicated that the character was dominant. Partial dominance was reported for this trait (Anonymous, 1976). Nayeem (1991) reported involvement of 2-5 genes in inheritance of this character. In the present study, additive gene action was predominant in both crosses (Table 34). Similar results were obtained by Patidar and Dabholkar (1981), Harer and Bapat (1982), Nagabasaiah (1982), Thombre *et al.* (1985), Palanisamy and Subramanian (1986), Chandrashekharappa (1987) and Senthil and Palanasamy

(1994). In contrast, others reported that dominant gene action was important. In the cross $S_1 \times R_2$, in the present study, dominance × dominance gene action was important, whereas significant additive × additive gene interaction was reported by Karale *et al.* (1984), Patil and Thombre (1985), and Thombre *et al.* (1985).

5.4.3 Panicle weight

Family means and generation mean analysis: The mean values of the F_1, BC_1 and BC_2 in both crosses were greater than both the parents indicating heterosis for this character (Table 33).

R^2 value for generation mean analysis for the cross $S_1 \times R_1$ was very low indicating that the model was not a good fit and that higher order interactions were involved for this cross (Table 34). In the cross $S_1 \times R_2$, (R^2 value was high) the dominance and dominance × dominance interactions were important. These estimates were in opposite directions implying the importance of duplicate type of epistasis. Similar results were reported by Harer and Bapat (1982), Patil *et al.* (1982), Deshmukh (1983), Thombre *et al.* (1985), Chhina and Phul (1988), Nimbalkar *et al.* (1988) and Rao *et al.* (1994). On the other hand, other workers reported additive and nonadditive effects to be important components for this character.

5.4.4 Primary branches

Family means and generation mean analysis: The mean values of F_1, BC_1 and BC_2 were greater than both parents, indicating heterosis for this character (Table 33). This shows overdominance to be important for this character. In $S_1 \times R_1$ cross, the R^2 value was very high while in $S_1 \times R_2$, it was very low indicating that the model was not a good fit for the latter cross (Table 34). Like panicle weight, dominance and dominance × dominance gene action was important in determining number of primary branches. The estimates were in same directions showing the importance of complementary epistasis. Harer and Bapat (1982), Patil *et al.* (1982), Deshmukh (1983), Thombre *et al.* (1985), Chhina and Phul (1988), Nimbalkar *et al.* (1988), and Rao *et al.* (1994) reported similar results.

5.4.5 Grain yield per plant

Family means and generation mean analysis: The mean values of F_1, BC_1 and BC_2 were greater than that of both the parents indicating heterosis for this trait (Table 33). The mean value of F_2 was on par with that of parents. This may be attributed to the fewer number of plants scored in other generations.

R^2 values obtained in both the crosses, $S_1 \times R_1$ and $S_1 \times R_2$, were high indicating that the model was adequate (Table 34). Also, dominance gene action was important in

these crosses. Similar results were reported by Harer and Bapat (1982), Kide *et al.* (1982), Nagabasaiah (1982), Patil *et al.* (1982), Kukadia *et al.* (1983), Berenji (1988), Chhina and Phul (1988), Yang (1991) and Gao (1993). In contrast, additive gene effects were reported for grain yield by Beil and Atkins (1967), Rao *et al.* (1968), Deshmukh (1983), Rao (1970), Patidar and Dabholkar (1981), Giriraj and Goud, (1982), Chandak and Nandanwankar (1983), Thombre *et al.* (1985), Shinde and Jagadeshwar (1986), Kulkarni and Shinde (1987), Mallick and Gupta (1988), and Spivakov (1988).

In this study additive × additive interaction effects and dominance × dominance effects were found important in both the crosses. Dominance × dominance interactions were reported by Indi and Goud (1981a and 1981b), Desai *et al.* (1985) and Patil and Thombre (1985). However, Rao *et al.* (1994) reported that all three epistatic interactions to be significant in the crosses.

In conclusion, among susceptible × resistant crosses, additive gene action was predominant for plant height and panicle length. Simple recurrent selection should work quite well to achieve desirable panicle length. The other characters, panicle weight, primary branches and yield per plant, showed dominance and duplicate type of gene action. It is difficult to fix such gene effects in inbred lines and is a time consuming process. The presence of dominance and duplicate epistasis would tend to retard the pace of progress through selection in early generations. Thus selection

for these characters would be more effective if the dominance and epistatic effects were reduced after a few generations of selfing.

In the present study, IS 14375, a red resistant (R_1) genotype and IS 14387, a brown resistant (R_2) genotype, showed consistent resistance over three years. In these genotypes, high resistance to grain mould is determined by both major and minor genes. The line, IS 14375, may contribute resistance to grain mould through major genes determining glume colour, high flavan 4-ols and phenols in seed besides minor genes for glume cover and seed hardness. On the other hand, IS 14387 has coloured glumes, high seed phenols, glume cover and hard seed contributing to grain mould resistance. Also, in the cross between IS 14375 (R_1) $\times$ IS 14387 (R_2), the F_2 and the backcross segregations indicated the involvement of at least three major nonallelic resistance genes besides minor modifiers. As such, these lines may be utilised as gene sources in the breeding programmes aimed at stable and long lasting resistance to grain moulds. Further, these resistant sources may be readily exploited in the breeding of coloured sorghum hybrids for industrial and export purpose.

Two white resistant sources, IS 25017, and IS 24495, showed inconsistent resistance over the years; and in these genotypes, resistance is governed predominantly by polygenes. Whereas, IS 25017 has coloured glume with high phenols and is hard seeded, IS 24495 has only hard seeds. Two moderately

resistant lines, GM 15018 and SP 33316, were also found inconsistent over the years. Segregation pattern and frequency distributions indicate that one of the dominant genes was contributed by the susceptible parents. Further, susceptible genotypes such as MS 422B and SP 33316, contributed positively towards resistance and thus may be utilised in improving grain mould resistance. It seems feasible to develop white hybrids with enhanced grain mould resistance from moderately resistant male steriles and restorer lines. Since additive gene effects were predominant, a simple recurrent selection might help in designing inbred lines with stable resistance. During this study, 20 agronomically elite advanced lines with white seeds and moderate grain mould resistance were obtained.

To get improved inbred lines with high levels of resistance to grain mould seems difficult and time consuming owing to the involvement of several major and minor genes. Also, the presence of dominance, epistatis and genotype × environment interactions for resistance as well as for other characters associated with grain mould resistance make the task complex. Quantitative trait loci (QTL) mapping is a highly effective approach for studying genetically complex characters such as grain mould resistance. Hopefully, with QTL mapping the role of specific resistance loci can be identified, race specificity of partial resistance genes can be assessed, and interactions among resistance genes, plant development and environment can be analysed.

Summary

6 SUMMARY

Sorghum (*Sorghum bicolor* (L.) Moench) is a staple food crop in the semi-arid tropical areas of Africa and India. It is also an important feed and forage crop in other parts of the world. In India, the development of short-duration and short-statured sorghum hybrids resulted in a quantum jump in productivity from 560 kg ha^{-1} in 1970 to 1020 kg ha^{-1} in 1996. However, yield potentials of sorghum hybrids are not fully realized as they are highly susceptible to grain moulds, which not only cause yield loss but also reduce grain quality and market value. For any effective *kharif* hybrid breeding programme, grain mould resistant male-sterile and restorer lines are essential prerequisites. Efficient exploitation of resistant genotypes in breeding grain mould resistant parental lines requires knowledge of the number and diversity of genes involved and of their mode of action in determining resistance.

The present investigation was undertaken with the following objectives: (1) To screen sorghum genotypes for grain mould resistance; (2) to evaluate sorghum genotypes for morphological and biochemical characters associated with mould resistance; (3) to estimate correlations between grain mould resistance, morphological and biochemical characters; (4) to determine the genetics and inheritance pattern of grain mould resistance; (5) to analyse the genetics of characters associated with mould resistance; and (6) to determine the genetics of

grain yield and yield components in grain mould susceptible × grain mould resistant crosses.

Twenty-two sorghum genotypes including released and prereleased varieties, restorers and nonrestorers, advanced breeding lines and other germplasm lines were evaluated for grain mould resistance under sprinkler irrigation during *kharif* 1994. They were also evaluated, in the same trial, for morphological and biochemical characters associated with mould resistance. The genotypes IS 14375, IS 14387, IS 18144, IS 18528, IS 24495, IS 25017 and B58586 recorded low mean field grade score (FGS) of 1.3 to 3.0, low threshed grade score (TGS) of 1.8 to 3.0, high germination percentage (83 to 94%) and low ergosterol content of 5 to 45 µg (g seed)$^{-1}$, and hence were classified as grain mould resistant. Ten genotypes 296B, SPV 462, SPV 475, MS 422B, AKMS 14B, AKR 150, R 1413, GM 15373, TNS 30 and GMRP 13, showed maximum susceptibility to grain mould and recorded high mean FGS and TGS (4 to 5), low germination percentage (6 to 52%) and high ergosterol content ranging from 70 to 253 µg (g seed)$^{-1}$. The remaining five genotypes were moderately resistant to grain moulds.

High phenol contents of 126 to 310 µg (g seed)$^{-1}$, in glumes and seed, were recorded in genotypes SP 33349, SP 33487, IS 14387, IS 14375, IS 18144, IS 18528. However, genotypes SP 33316 and GM 15018 recorded high phenols in glumes only. Flavan-4-ols in glumes and seed were detected in a few genotypes

such as IS 14375, IS 18144, IS 18528 and SP 33349, and in substantial quantity in the glumes of SP 33316. Most of the resistant genotypes, *viz.,* IS 14375, IS 14387, IS 18528, IS 24495, IS 25017, IS 21443, SP 33349 and B58586 were relatively hard seeded taking 5 to 6.78 sec to grind in a Stenvert hardness tester. Percentage glume cover varied from 25 to 90%. Out of 22 genotypes, 11 had straw-coloured glumes, 7 had dark-coloured glumes and 4 had light-coloured glumes. Only a few lines, *viz.,* IS 14375, IS 14387, IS 18144, IS 18528, SP 33349 and SP 33487, had coloured seeds.

Correlations between grain mould resistance and 17 associated characters were estimated in the same 22 genotypes. Field grade score (FGS) showed strong positive correlation with threshed grade score ($r = 0.93$) and ergosterol content ($r = 0.78$), and strong negative correlation with germination percentage ($r = -0.84$), seed hardness ($r = -0.79$), glume colour ($r = -0.75$), and seed colour ($r = -0.66$). Field grade score also showed significant negative correlation with acid-methanol extract of glume phenols ($r = -0.51$), seed phenols (both methanol and acid-methanol extracts), flavan-4-ols in glumes, and percentage glume cover. Further, field grade score showed significant positive correlation with grain yield per plant and significant negative correlation with plant height.

All the other grain mould measuring variables, *viz.,* threshed grade score (TGS), percentage seed germination and ergosterol, in general, showed similar correlations

to those shown by FGS. Strong negative correlations of FGS and TGS with glume colour (r = -0.400 and -0.492, respectively) were also observed in 225 F_2 progenies of a cross between lines with straw (AKMS 14B) and purple (IS 14375) glumes.

An overview of the means and correlations indicates that seed hardness, glume colour, seed phenols, seed flavan-4-ols and glume cover, in association with one another, bring about high resistance to grain moulds. Thus manipulation of some of these characters may help in breeding resistant genotypes. The tannins in brown sorghums are polyphenols, which render the grain astringent and unpalatable. High tannin levels result in low digestibility and reduced protein efficiency ratio and thus present problems of utilisation of brown-coloured seed. Glumes with intense red and purple colour have a tendency to stain the sorghum kernels in humid conditions. Threshing is difficult in sorghum lines with long enclosed glumes; in guinea sorghums, glumes cover the seed up to physiological maturity and open up only at the time of harvest. Very hard seeds have low digestibility and are not suitable for some food preparations. Hence it is important to strike a balance between the level of grain mould resistance and grain hardness. Thus breeding for light glume colour with high levels of glume flavan-4-ols, moderate seed hardness, glume cover up to 30 d after anthesis along with free threshing might result in mould resistant lines with desirable grain quality.

On the basis of evaluation for grain mould resistance during *kharif* 1994, three susceptible and five resistant genotypes were selected for inheritance studies. The genotypes AKMS 14B, MS 422B and AKR 150 were consistently susceptible and IS 14375 and IS 14387 were consistently resistant over the years studied. However, white resistant and moderately resistant sources, IS 25017, SP 33316 and GM 15018, were scored resistant/moderately resistant during *kharif* 1994, susceptible during *kharif* 1995 and moderately resistant during *kharif* 1996. The post-maturity period, i.e., 30 to 50 d after anthesis of IS 25017 (R_3) white resistant source, coincided with heavy rainfall weeks during 1995 and low rainfall weeks during 1996. Accordingly, the mean FGS of R_3 was high during 1995 and moderate during 1996. It appears that the white resistant sources are rather unstable and the FGS reaction of such genotypes depends on the level of ambient humidity during the post-maturity period.

Crosses between susceptible × resistant genotypes, their F_2 and backcross generations were evaluated for grain mould resistance and associated characters during 1995 and 1996. Genetics of the traits studied was inferred from the family means, frequency distributions and generation mean analysis. For grain mould resistance, the F_1 means in most of the crosses between white susceptible × coloured resistant lines tended towards the resistant parent. In a white susceptible × white resistant cross, the F_1 mean was equal to midparent value during 1995 and tended towards resistant parent during 1996. In a red resistant × brown resistant

cross, the F_1 mean was greater than that of both the parents but was still in the resistant range, and in a white susceptible x moderately resistant cross the F_1s exhibited greater resistance than both the parents. All these results indicate the dominance of grain mould resistance over susceptibility. The inconsistent inheritance pattern observed over years in different crosses may be attributed to the diverse resistance genes that specify different mechanisms of resistance to grain mould.

Frequency distributions for FGS and TGS were bimodal or unimodal with small peak at the tail giving an indication of a second mode, suggesting that both major and minor genes control grain mould resistance. The F_1 and F_2 distributions skewed towards the resistant parent and those of BC_1 and BC_2 overlapped with those of recurrent parent. Inconsistent frequency distributions in different crosses for FGS and TGS over two years suggest that a number of major genes in conjunction with minor modifiers determine grain mould resistance.

Segregation patterns in three white susceptible x red resistant crosses showed resistant F_1s and F_2s segregated into 9 resistant (R) : 7 susceptible (S) indicating digenic inheritance with duplicate recessive epistasis. In three white susceptible x brown resistant and one brown resistant x white resistant crosses, the F_1 hybrids were resistant and F_2s segregated into modified trigenic ratios of 39R:25S, 45R:19S, 27R:37S and 27R:37S, respectively. In the red resistant x brown resistant cross, the

F_2 segregation fitted 57R:7S trigenic ratio, suggesting the involvement of three major nonallelic genes for grain mould resistance. Also, in one white susceptible (S_2) x red resistant (R_1) cross, the F_2 segregated into 51R:13S trigenic ratio.

From these segregation patterns of modified dihybrid and trihybrid ratios, observed in different crosses, it may be concluded that diverse nonallelic dominant genes are determining grain mould resistance. One to two basic dominant genes from the resistant parent and one dominant gene contributed by the susceptible parent might interact to produce grain mould resistance. The dominant gene from the susceptible may be different in different susceptibles or is modified to behave differently in different parents.

For grain mould resistance, good fit of the genetic model was obtained in generation mean analyses of all the crosses, as indicated by the high R^2 values (83 to 99%) obtained. Additive effects were significant in all the crosses grown during 1995 and 1996. Negative dominance effects were also observed in five crosses which were important in three of these crosses. All the three-gene interactions were found important in various crosses. Although fixable additive gene effects were present in almost all the crosses, the presence of dominance and complementary epistasis would tend to retard the progress through selection in earlier generations. Thus selection for grain mould resistance would be more effective if dominance and epistasis effects were reduced after a few generations of selfing.

Estimates of genotype x environment interaction for grain mould resistance, from pooled data of 1995 and 1996, in six crosses were obtained by the weighted least squares method. Important additive and dominance gene effects of approximately equal magnitude were observed. Environmental effects were significant but of lesser magnitude and environment x dominance (ExH) interactions were also significant in white susceptible x white resistant, brown resistant x white resistant and red resistant x brown resistant crosses.

From the overall results of family means, frequency distributions, segregation pattern and generation mean analysis, it may be concluded that grain mould resistance is governed by various major genes which are modulated by several minor modifiers. In general, additive and dominance gene actions were found predominant. Environment and environment x dominance interactions, though of lesser magnitude, nevertheless influenced various crosses involving IS 25017, a white resistant line (R_3) as one of the parents.

For days to 50% flowering, the F_1 mean value tended towards the early parent in all but 2 of the 18 crosses studied, indicating dominance of earliness. The mean values of BC_1 and F_2 tended towards the early parent confirming dominance of earliness. Frequency distributions in F_2 for days to flower showed bimodal to pentamodal distributions indicating the involvement of more than two genes. Generation mean analysis showed high R^2 values in all the crosses grown during 1995 and 1996, and

additive gene effects were of prime importance in both the years. Also, positive additive x dominance interactions were observed. Although, additive gene action and its first order interaction are fixable, epistatic gene effects cannot be utilised as they operate in opposing directions. It may be necessary for selection pressure to be lenient in earlier selfed generations and intensified later when homozygosity is approached. Breeding procedures to be followed for grain mould resistance and earliness seem to be the same in susceptible x resistant crosses.

For seed colour, in all white x red crosses the F_1 mean value was greater than that of the red parent. In the red x brown cross, the F_1 mean was greater than that of both the parents and in the white x brown crosses the F_1 mean tended towards the brown parents. The frequency distributions of F_2 showed 2 to 3 peaks giving an impression of bimodal distribution. Generation mean analysis showed that dominance gene action was the most important gene effect. Dominance x dominance interactions were also found important for seed colour. These results indicate that a resistant coloured hybrid is easy to produce.

For glume cover, the mean values of F_1 and F_2 were greater than the mean value of both parents in most of the crosses. The frequency distributions for glume cover in three crosses were bimodal, suggesting the involvement of major genes. In other crosses, normal symmetrical distributions were observed indicating polygenic inheritance. R^2 values for all crosses, except one, were very high ranging from 81 to

99%. Dominant gene action was found most important and significant. Additive gene action was also found in all the crosses but was of lesser magnitude. Dominance × dominance and additive × dominance interactions were important but lesser in magnitude than dominance gene effects in determining glume cover. The dominance effects may be utilised in hybrid breeding programme, and to obtain inbred line, selection pressure can be relaxed in early selfed generations and intensified later when homozygosity is approached.

For glume colour, the means of F_1 and F_2 of a cross between straw coloured × purple glumed lines tended towards the midparent value. F_2 distribution showed four modes, suggesting the involvment of major genes. Additive gene action was the most important significant gene action observed. Simple recurrent selection should work quite well to achieve desirable glume colour.

Generation mean analysis studies were also conducted for grain yield and yield components in two susceptible × resistant crosses. Additive gene action was predominant for plant height and panicle length; hence recurrent selection should work quite well to achieve desirable panicle length. Dominance and dominance × dominance interactions were found important for panicle weight, primary branches and grain yield per plant. It is difficult to fix such gene effects in inbred lines and is a time consuming process. The presence of dominance and duplicate epistasis would tend to retard the pace of progress through selection in early generations. Thus

selection for such characters would be more effective if the dominance and epistatic effects were reduced after a few generations of selfing.

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