

SÉLECTION DU MIL À CHANDELLE
POUR LA RÉSISTANCE AUX MALADIES
ET AUX RAVAGEURS

Résumé

Etude de l'état actuel de la lutte contre les agents biologiques responsables des pertes de rendement du mil à chandelle. Etude des possibilités de lutte contre les maladies, les insectes ravageurs, les mauvaises herbes et les oiseaux granivores, par la sélection de cultivars possédant une résistance durable. Les recherches futures sur la sélection du mil à chandelle doivent notamment viser à déterminer la nature et les possibilités de la transmission héréditaire de la résistance aux maladies; à mettre au point des stratégies pour accroître la durée de la résistance aux maladies; à rechercher les possibilités de dresser des barrières complexes multiples contre les agents phytopathogènes; à intensifier les prospections et à mettre en œuvre des techniques efficaces de détermination de la résistance aux insectes ravageurs; à évaluer les stratégies de lutte intégrée contre les insectes; à mettre au point des techniques de criblage pour identifier et sélectionner des cultivars résistants à *Striga*; à rechercher des pratiques culturales et des techniques permettant de combattre la *shibra*.

SELECCIÓN DE RESISTENCIA A LAS
ENFERMEDADES Y PLAGAS DEL MIJO PERLA

Resumen

Se examina la situación actual de la lucha contra los agentes biológicos causantes de pérdidas en el rendimiento del mijo perla. Se estudian las posibilidades de acción contra las enfermedades, las plagas de insectos, las malas hierbas y las aves granívoras mediante la introducción de cultivares con resistencia duradera. En las futuras investigaciones sobre fitogenética de este cultivo es preciso hacer hincapié en los siguientes puntos: evaluación de la naturaleza y herencia de la resistencia a las enfermedades; elaboración de estrategias para aumentar la duración de la resistencia a las enfermedades; investigaciones sobre la posibilidad de utilizar barreras múltiples complejas frente a los patógenos; encuestas complementarias y preparación y utilización de técnicas eficaces de selección para las plagas de insectos; evaluación de estrategias de lucha integrada contra los insectos; elaboración y utilización de técnicas de selección para descubrir y desarrollar cultivares resistentes a la mala hierba *Striga*, e investigación de las prácticas de cultivo y técnicas de fitogenética para la lucha contra la *shibra* en el África saheliana.

Breeding for disease and pest resistance in pearl millet

R.J. WILLIAMS and D.J. ANDREWS

Summary. The present status of the control of biological agents causing yield losses in pearl millet is reviewed. The possibilities of controlling diseases, insect pests, weeds and grain-eating birds by breeding cultivars with durable resistance are discussed. In future breeding research in this crop, areas needing to be emphasized include: evaluation of the nature and inheritance of disease resistance; development of strategies to increase the durability of resistance to diseases; investigations into the possibility of using complex multiple barriers to disease pathogens; additional survey work and the development and use of effective screening techniques for insect pests; evaluation of integrated control strategies against insects; development and use of screening techniques to identify and develop cultivars resistant to witchweed; and investigation of cultural practices and breeding techniques to control *shibra* in Sahelian Africa.

Pearl millet, *Pennisetum americanum* (L.) Leeke (syn. *Pennisetum typhoides* (Burm.) Stapf. and Hubb.), is the staple cereal of many millions of the world's poorest people in the semi-arid regions of tropical and subtropical developing countries in Asia and Africa. In India, about 14 million ha of pearl millet are cultivated annually, primarily in the northern and western states of Rajasthan, Maharashtra, Gujarat, Uttar Pradesh and Haryana (about 87 percent of the national total), with important production areas also in Andhra Pradesh, Karnataka and Tamil Nadu in the south (see Table 1 and Fig. 1). In Africa, the pearl millet crop is of most importance in the Sahel, with each of the seven countries in this region growing about one million ha or more of pearl millet annually and collectively growing about 14 million ha each year (see Table 2 and Fig. 2). Other important pearl millet-growing regions occur in eastern and southern Africa, though in these regions other millets, such as finger millet (*Eleusine coracana* Gaertn.), contribute significantly to the FAO production data generally listed under the heading of "millet" (FAO, 1981).

The authors are with the Pearl Millet Improvement Programme, International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru PO, Andhra Pradesh 502 324, India. This article is based on a paper presented at the FAO/ITA Expert Consultation on Durable Resistance Breeding, Ibadan, Nigeria, 23-29 October 1982.

In African countries and in India, the national average grain yields of pearl millet are generally in the low range of 400-600 kg per ha (FAO, 1981), and in some African countries where pearl millet is a major crop the average yield is less than 400 kg per ha (see Table 2). On experiment stations, however, yields of 2-3 tonnes per ha are regularly reported (ICRISAT, 1976, 1977, 1978, 1981), and undoubtedly many farmers occasionally achieve yields in the 1-2 tonne-per-ha range with traditional varieties when conditions are highly favourable for the crop in a particular season.

The basic objective of the Pearl Millet Improvement Programme being carried out at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) is to develop technology that will ultimately enable farmers in the semi-arid tropics to achieve higher yields more consistently from their pearl millet crops. The first step in this process has to be identification of the major constraints on increased production, followed by the development of effective and acceptable measures to reduce or eliminate those constraints. For pearl millet in the semi-arid tropics, the abiotic environmental factors of moisture stress and low fertility are undoubtedly major contributory-factors to low grain production, together with the biotic factors of diseases, insect pests, parasitic and non-parasitic weeds and the inherent low productive capacity of some traditional cultivars. For the improvement of pearl

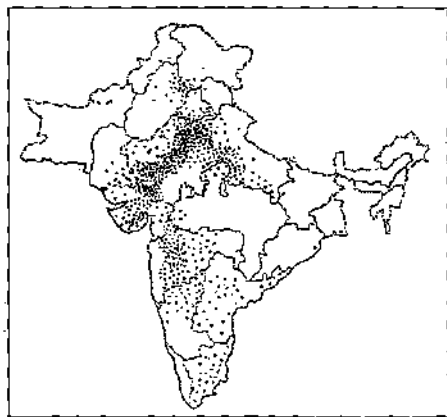


Figure 1. Reported area planted to pearl millet in southern Asia in 1978 (one dot equals 20 000 ha)

millet production all these factors need attention and their interactions with sociological, economic and political factors need to be recognized and dealt with. This article confines itself to discussing the control of the biotic yield reducers by breeding cultivars resistant to diseases and pests.

Pearl millet origins, distribution and breeding system

This crop appears to have been domesticated along the southern margins of the Saharan highlands, between 3000 and 4000 BC, and today its main centre of diversity occurs in the Sahelian zone of Africa between Senegal and central Sudan (Brunken, de Wet and Harlan, 1977). Migration and trade caused the crop to spread to southern Europe, the Kingdom of Saudi Arabia, eastern and southern Africa and the Indian subcontinent probably by the beginning of the Christian era (Rachie and Majumdar, 1980) and to the Americas probably in the middle of the nineteenth century (Ball, 1903). Subcentres of diversity exist in regions where the crop has evolved over long periods in response to local selection pressures, e.g. the longer days experienced in northern India.

TABLE 1. Area cropped with pearl millet in 17 states in India in 1973-74

State	Area (1 000 ha)	State	Area (1 000 ha)
Rajasthan	5731	Punjab	147
Maharashtra	2215	Delhi ¹	22
Gujarat	2149	Bihar	16
Uttar Pradesh	1063	Jammu and Kashmir	15
Haryana	956	Orissa	4
Karnataka	610	Pondicherry ¹	1
Andhra Pradesh	582	West Bengal	0.4
Tamil Nadu	401	Himachal Pradesh	0.01
Madhya Pradesh	218		
		Total	14 130

Source: Indian Agricultural Statistics, 1973-74
1 Union Territory



Figure 2. Reported area planted to pearl millet in Africa in 1978 (one dot equals 20 000 ha)

Since introductions to the Americas and Australia are fairly recent they constitute a somewhat relatively narrow genetic base.

Pearl millet is hermaphroditic, with pronounced protogyny, which produces up to 70-80 percent cross-pollination (Rachie and Majmudar, 1980). In its centre of origin and diversity (Sahelian Africa) it freely crosses with its wild progenitors (*Pennisetum violaceum* and *P. fallax*), producing the mimetic weed shibra,

Which persists in the cultivated crop (Brunken, de Wet and Harlan, 1977). The highly outcrossing nature of the crop has important implications for breeding for stable disease resistance and for increased vulnerability to floral diseases in F_1 hybrids.

In the United States and India, cytogenic male sterility has been used to produce F_1 hybrids (Rachie and Majmudar, 1980). In India, hybrids have been selected for increased grain production and are now being grown there on more than one million ha per annum.

Biotic yield reducers

Diseases. More than 50 fungal, bacterial and viral pathogens of pearl millet have been reported (Ramakrishnan, 1971; Ferraris, 1973). However, the pathogens that cause major damage to the crop are much fewer.

The most important disease in Africa and Asia is downy mildew, caused by *Sclerospora graminicola* (Sacc.) Schroet. In India, this disease occurred in epidemic proportions in the early 1970s and devastated the hybrid crop, which was cultivated on more than one million ha (Safeulla, 1977). It also destroys much pearl millet every year in Africa (Delassus, 1964; King and Webster, 1970; Jouan and Delassus, 1971; Girard, 1975; Williams, 1984).

Ergot, caused by *Claviceps fusiformis* Lovell, can incite severe disease on hybrid millet

TABLE 2. 1980 millet production data for countries in Africa with at least 0.1 million ha in millet¹

Country	Area of millet cultivation (million ha)	Average yield (kg/ha)	Country	Area of millet cultivation (million ha)	Average yield (kg/ha)
Nigeria	5.03	636	Zimbabwe	0.38	474
Niger	3.07	446	Ethiopia	0.27	724
Mali	² 1.40	536	Ghana	0.24	273
Sudan	1.30	346	United Rep. of Tanzania	0.22	727
Chad	21.15	522	Egypt	² 0.17	³ 3734
Senegal	20.95	684	Togo	20.17	724
Upper Volta	0.90	444	Zambia	0.13	462
Uganda	0.55	818	Mauritania	² 0.10	190
Rep. of Cameroon	² 0.45	889	Africa total	(17 079)	(666)

¹ Source: FAO (1981). FAO Production yearbook 34:106. ² These 'millet' data appear to include sorghum data, as there are no separate sorghum data for these countries in the relevant section of the FAO Production Yearbook. In Egypt, Mali, Togo and the Republic of Cameroon the sorghum values are likely to have been substantial proportions of the figures given for millet. - ³ This value almost certainly includes yields from irrigated sorghum.

in India (Safeeulla, 1977; Arya and Kumar, 1982), particularly when rains occur during the flowering period. It is generally less of a problem in open-pollinated traditional cultivars. In eastern Africa, however, ergot is important in open-pollinated varieties and in West Africa it can be devastating on short-duration, photo-period-insensitive cultivars. Ergot is also important because the alkaloid-containing sclerotia of this pathogen contaminate grain, thus creating a health hazard for consumers.

Smut, caused by *Tolyposporium penicillariae* Bref., can cause serious damage in northern India and West Africa. As with ergot, F₁ hybrids appear to be more susceptible to smut than open-pollinated varieties.

Of the leaf diseases, rust, caused by *Puccinia penniseti* Zimm., is potentially important in southern India and eastern Africa. Severe outbreaks of blast, caused by *Pyricularia setariae*, have occasionally been reported in northern India.

Less important, although potentially damaging, diseases include seedling blights (*Helminthosporium* spp. and *Fusarium* spp.) and certain leaf spots, such as zonate leaf spot (*Gloeocercospora* sp. and *Dactuliophora elongata* Leakey), curvularia leaf spot (*Curvularia penniseti*) and cercospora leaf spot (*Cercospora fusimaculans* Atk.) (Rachie and Majmudar, 1980).

Most of the research published on disease resistance in pearl millet has been performed in India, where the diseases considered important enough to warrant control through resistance breeding are downy mildew, ergot and smut (Williams, Singh and Thakur, 1982). Downy mildew has received most attention in the past ten years, with ergot and smut now following close behind. These three diseases cause significant yield losses. While ergot and smut attack mainly hybrids, they also attack varieties if rains are frequent during flowering. The damage caused by the leaf diseases is not usually severe and depends on the stage of crop development. There is a need for studies on the relationships between incidence and severity of the leaf diseases at various stages of crop development and yield reduction.

Insect pests. About 300 insects have been reported to feed on pearl millet in different parts of the world (Sharma, Davies and Arora, 1981), but the number that can cause serious damage is probably no more than a dozen, and those causing serious damage on a consistent annual basis are much fewer (Verma, 1980).

Several polyphagous insects, such as locusts and grasshoppers (*Schistocerca gregaria*, *Locusta migratoria* and *Chrotogonus* spp.), army-worms (*Mythimna* spp. and *Spodoptera exempta*) and *Heliolithis armigera*, sporadically cause severe damage in pearl millet, but these insects are probably best held in check by using insecticides.

There are reports of serious damage to pearl millet in northern India by white grubs (*Holotrichia* (*Lachnosterna*) *consanguinea* Blanch), particularly in the states of Rajasthan and Gujarat (Gahukar and Jotwani, 1980; Rachie and Majmudar, 1980) and the authors have seen patches of pearl millet in farmers' fields and entire fields on experiment; stations killed before flowering time by white grubs in Rajasthan. The shootfly (*Atherigona approximata* Mall.) kills the central whorl leaf, particularly in later sown crops, but generally the plants grow so rapidly that the larvae are not able to kill the growing point. However, when conditions preclude rapid growth, dead hearts or damaged inflorescences may occur and yield losses in the range of 20 to 60 percent have been reported (Natarajan *et al.*, 1973; Gahukar and Jotwani, 1980). Other insect pests reported to cause occasional damage to pearl millet in India are the midge *Genomyia penniseti* Felt. and various sucking insects, such as *Pyrilla perpusilla* Walk., *Rhopalosiphum maidis* Fitch, *Empoasca* spp., *Aphanus sardidus* and *Myllocerus* spp. However, at the present time the only serious pest that seems to warrant major control efforts in India is the white grub. The other insects mentioned are potentially serious pests and new varieties should be checked for high levels of attack by particular insects under natural field conditions.

In Africa, the stem borers *Acigona ignefusalis* and *Sesamia calamistis* are reported as pests on pearl millet in the Sahelian and

Sudanese zones, with the former pest being the more important (Harris, 1962). The millet earhead caterpillar (*Rhaguvia albipunctella*) was very destructive in the Sahelian regions of West Africa in the early 1970s, with estimated losses of up to 50 percent being reported (Vercombe, 1978; Ndoye, 1979). The midge *G. penniseti* has also been reported to cause severe grain yield reduction of mid-season Souma millets, which flower in late September in Senegal (Coutin and Harris, 1968). In the ICRISAT Millet Entomology Programme for West Africa, based at the ICRISAT Sahelian Centre in the Niger, research priority is being given to *A. ignefusalis* and *R. albipunctella* (Nwanze, 1982). A multi-faceted integrated control programme is envisaged, with host-plant resistance being a major component.

Parasitic weeds. Of the several witchweeds (*Striga* spp.) known to occur in Africa and Asia, *S. hermonthica* is the most serious parasitic weed on pearl millet in Africa and causes severe losses in the Sahelian region. *S. asiatica* appears to be the most common in India and southern Africa (Rachie and Majmudar, 1980), though there are few reports of this weed as a serious problem in pearl millet. In sorghum, however, the cultivation in India of new hybrids highly susceptible to *S. asiatica* has resulted in an alarming increase of this parasite and a change to other crops on land traditionally used for growing sorghum (House and Vasudeva Rao, 1982).

Large areas of pearl millet in the Sahel have been devastated by *S. hermonthica*. In the authors' opinion, it is essential to find the sources of resistance to this weed pest in order to improve cultivation of pearl millet in the Sahel.

Non-parasitic weeds. Weeds should obviously be controlled in all crops (especially during the early stages of crop development) if the yield potential is to be achieved. There is, however, a special and important weed problem affecting pearl millet in Sahelian Africa that is much more difficult for farmers to control than the conventional weed problem. This is the pres-

ence of shibra, which mimics the pearl millet plant in appearance but is virtually non-productive in terms of harvestable grain. Because it is a mimetic weed, it escapes removal during the normal weeding processes, persists in the crop, competes for environmental resources and contributes pollen to the varietal gene pool. At maturity, shibra heads shatter and disperse their seeds to reinfest the fields. The authors have seen up to 20 percent of shibra in farmers' fields in West Africa and believe it to be a general and serious problem throughout the region.

Control of the shibra problem needs a combination of cultural and plant-breeding activities. Shibra plants should be rogued prior to anther shedding, and shibra gene contamination needs to be eliminated from local cultivars through breeding.

Birds. Flocks of grain-eating birds consume vast amounts of pearl millet grain annually in India and Africa. In India, sparrows (*Passer domesticus* L. and *Gymnorris xanthocallis*), parakeets (*Psittacula* sp.) and crows (*Corvus* sp.) are probably the most important bird pests (Rachie and Majmudar, 1980). In Africa, where birds are believed to be the most serious pest of millet (Rachie and Majmudar, 1980), the principal pest is the weaverbird (quelea, *Quelea quelea* L. in the Sahel, *Q. quelea aethiopica* Sundeval in mountainous areas of eastern Africa, *Q. quelea centralis* Van Someren in East Africa and *Q. quelea lathami* Smith in southern Africa).

It is debatable whether any degree of bird control can be achieved with genetic characters of the host plant (heavily awned millet may be subject to less attack, but there are conflicting reports on the effectiveness of this character); to date it would appear that the most effective method of discouraging birds is to scare them off by traditional methods. In West Africa, an international effort against bird pests — the Organisation commune de lutte antiacridienne et de lutte antiaviaire (OCLALAV) — has been operating for some time and uses various methods of bird destruction, including fire and explosives to destroy nesting colonies and

spraying of poisons such as parathion and phosdrin (Pradat, 1962; Bruggers and Jaeger, 1982). Such communal action needs to be continued in West Africa and strengthened in eastern and southern Africa, where the depredations of migratory birds cause enormous grain losses annually (Bruggers and Jaeger, 1982).

The need for and use of surveys. More precise information is needed on the incidence, severity and losses caused annually by pathogens and pests of pearl millet, particularly in Africa. A great deal of this information can be collected in the Sahel during the first phase of the FAO Integrated Pest Control Project, and similar activities are needed in eastern and southern Africa. In India, there appears to be more monitoring of problems in pearl millet, though there is a need to establish a more precise national pest and disease monitoring system for this crop.

A few notes of caution are pertinent on the use of information from surveys. First, in order to translate incidence and severity data into meaningful yield loss data, the relationships between these parameters need to be determined through experimentation. Moreover, while surveys will indicate the present problems (with traditional cultivars and cultural practices) they do not necessarily indicate what new major problem might emerge as a result of the introduction of new varieties and cultural practices (e.g. ergot was regarded as a minor problem on pearl millet in India prior to the large-scale use of F₁ hybrids). Thus, the most important potential pest and disease problems also need to be identified from survey work and new genotypes should be exposed to these prior to large-scale introduction. Even then, not all potential problems will be identified and vigilance will be needed during the introduction phase of new genotypes and cultural practices, particularly if exotic parent material has been used.

Despite a lack of knowledge about the occurrence of and losses caused by pathogens and pests in pearl millet, there are problems so severe that their control is known to be of primary importance for increasing production. In

Sahelian Africa these are grain-eating birds, downy mildew, witchweed and probably *Acigona* stem borer and *Rhaguya* earworm; in India they are downy mildew, ergot, smut and probably white grubs in the northwestern states of Rajasthan and Gujarat. Host plant resistance will have to be the major defence against downy mildew, witchweed, ergot, smut, stem borer and *Rhaguya* earworm, although the integration of appropriate cultural and chemical control measures needs to be investigated in order to make the control more effective and more durable.

Resistance screening techniques

The rate of progress that can be made in the improvement of a crop for any genetic character will depend primarily on the effectiveness of the screening technique. In projects on identification of disease and pest resistance, considerable attention needs to be given at the outset to ensure that the screening techniques are reliable and relevant. Reliability requires that adequate levels of inoculum be provided uniformly throughout the populations of plants being screened and that environmental parameters be maintained within a range conducive to infection/infestation and disease/damage development. Relevancy requires that the host be challenged by the pathogens or pests in as natural a way as possible, and this will in turn require a sound knowledge of the biology, epidemiology and bionomics of the pathogens and pests and the diseases and damage that they cause. The requirements of reliability will generally preclude a completely natural means of host challenge, but highly artificial methods of inoculation/infestation and plant maintenance should generally be avoided if reactions are to be obtained that have relevance to the crop growing in the field.

A second important aspect of screening is the method used to assess plant varietal reactions. Standard rating scales are essential to provide objectivity on the part of workers and from season to season. It should be clearly recognized, however, that as pearl millet is a highly outcross-

ing crop, with considerable variability occurring within cultivars, valuable sources of resistance can be identified within populations that are generally susceptible. Thus, as long as a reliable screening technique has been employed, ratings of varietal reaction should be made on individual plants within test lines in order to evaluate the potential for selection within lines.

Downy mildew. The traditional method of screening for resistance to downy mildew in pearl millet was to plant the test material in a "sick plot", i.e. a field plot into which zoospore-containing crop debris had been incorporated (Chahal *et al.*, 1975; Deshmukh, More and Utikar, 1978). The use of a sick plot, however, has several drawbacks (Williams, 1983) and a more efficient and reliable resistance screening technique was developed in the mid-1970s in which test lines were challenged by zoospores from sporangia produced on highly susceptible "infecter rows" planted throughout the screening area (Williams, Singh and Pawar, 1981; Williams, 1984).

Two basic parameters have been used to define susceptibility (or, conversely, resistance) to downy mildew in pearl millet. The most frequently used is the percent incidence of plants that show systemic symptoms, irrespective of the severity of symptoms on individual plants. Arbitrary figures have then been established below which the variety is regarded as resistant. The data for the incidence score can be collected easily and rapidly in the field and this method is probably the most practical one when large numbers of breeding lines are being screened. In order to obtain an accurate incidence score at the end of the season it is necessary to score the crop more than once.

The second scoring system that has been used combines disease incidence and severity into a disease index (Williams and Singh, 1981). This rating is done only once, after flowering, and thus needs to be combined with an earlier incidence score, as described above. The latter method is more laborious than the incidence method, but it does provide a more accurate measure of the amount of disease. This is

important for evaluating relationships between disease and yield (Williams and Singh, 1981) and for studies on the possible occurrence of partial resistance.

Ergot. Suspensions of conidia from fresh honeydew produced on pearl millet are the most effective inocula for inducing ergot in this crop. The optimum flowering stage for inoculation is when the greatest flush of fresh stigmas occurs on the inflorescence. However, if the stigmas receive pollen before or at the same time as inoculum, the pollen predominates and little ergot will develop (Thakur and Williams, 1980). Thus, in screening for ergot resistance, it is not possible to rely on a completely natural system of plant challenge by inoculum produced on interplanted inoculum donor plants, because it is essential to ensure that inoculum precedes pollen in reaching the stigmas. This is best achieved by a system of bagging tillers at crucial stages. The elimination of pollen interference should be combined with uniform inoculation, using viable inoculum to avoid high frequencies of escapes (Thakur, Williams and Rao, 1982).

A rapid and reliable method of assessing the proportion of infected florets on an inflorescence, which utilizes a set of standard drawings of pearl millet inflorescences with various proportions of infected florets from one to 90 percent, has been devised (Thakur and Williams, 1980).

Smut. Although there is still a great deal to be learned about the epidemiology of pearl millet smut, which is incited by *Tolyposporium penicillariae*, it has long been known that floret infection is effected directly by airborne sporidia produced by germinating sporeballs and not as a result of systemic colonization of the plant (Bhat, 1946). Various workers have tried direct inoculation of inflorescences, generally by injection at the boot-leaf stage of development with aqueous suspensions of sporeballs and/or sporidia, with conflicting results (Patel and Desai, 1959; Husain and Thakur, 1963; Pathak and Sharma, 1976a; Bhowmik, and Sundaram, 1971). All these

authors indicated the important role high humidity plays in causing infection.

In more recent studies, Thakur, Subba Rao and Williams (1982) evaluated several aspects of smut-inoculation methods and concluded that the most effective and reliable method was injection of a fresh sporidial suspension (ca. 1×10^6 sporidia/ml) into the boot just prior to inflorescence emergence, immediate bagging of the inoculated tillers and provision of high humidity for the period from inoculation to symptom appearance. The rating of the reactions of plants inoculated with *T. penicillariae* includes combinations of incidence and severity. As for ergot, standard drawings have been developed to assist in the estimation of the proportion of diseased florets on individual inflorescences (Thakur and Williams, unpublished data). The mean and range of severity within test lines provide valuable selection criteria.

Foliage diseases. Foliage diseases have been studied much less than the three diseases referred to above. Those that have received most attention are rust and blast, with occasional reports of work on resistance to other pathogens such as *Helminthosporium rostratum* Dreschler (Singh, Choudhary and Bhatnagar, 1980) and *Cercospora penniseti* (Burton and Wells, 1951). In screening for blast and rust resistance, most workers have relied on natural infection in the field (Pathak *et al.*, 1976; Duhan and Thakur, 1980; Williams, Singh and Thakur, 1982), but Yadav, Agnihotri and Prasada (1980) inoculated seedlings with a "highly pathogenic strain" of the blast fungus in a greenhouse test.

Rust and blast are diseases in which "infector rows" have been effectively used to provide uniform inoculum for resistance screening in other cereal crops, and there is no reason to believe that such screening would be less effective in pearl millet. The critical factors that need to be determined in order to use the infector-row screening technique effectively are the environmental conditions conducive to sporulation and infection and the required time and spatial distribution of infector and test rows.

The rating of reactions of cereals to leaf diseases is fraught with pitfalls and difficulties. The main questions are: at what growth stage(s) should the assessments be made; on which leaves; in what way; how does one cope with variability in time of flowering among the test lines; and, can epidemiologically important parameters be measured? These questions can only be answered effectively if there is sound knowledge available as to the biology and epidemiology of the disease and of its effects on plant development and yield. Many foliage pathogens can quickly colonize senescing leaf tissue, and thus ratings made too late in the maturity of a line will overestimate its susceptibility. Conversely, ratings made too early in the maturity of a line will underestimate its susceptibility to certain diseases. Accordingly, lines with variable flowering and maturity dates should be scored at a fixed physiological development event and not chronologically.

Multiple disease resistance. Since effective, reliable screening techniques have been developed for the three major diseases (downy mildew, ergot and smut) it has become possible to screen for sources of multiple disease resistance. This is done by subjecting the same plants to several pathogens and selecting individuals that carry resistance to all the diseases.

Screening for combined resistance to downy mildew, ergot and smut in multiple inoculation trials was begun at ICRISAT in 1982 (Williams *et al.*, unpublished data). The selected test lines, elite progenies from the ergot and smut screening projects, were grown in the downy mildew nursery (Williams, Singh and Pawar, 1981) and, at the boot-leaf stage, tillers of selected downy mildew-resistant plants were inoculated with sporidial suspensions of *Tolyposporium penicillariae*, other tillers were bagged to be inoculated later with fresh honeydew suspensions of *Claviceps fusiformis* and still others were bagged with no inoculation carried out. Downy mildew-resistant plants were screened in this way for ergot and smut resistance; they were selfed so that selfed seed could be harvested from individual plants with multiple resistance.

Insect pests. The authors are unaware of any studies in which pearl millet has been effectively screened for resistance to any insect pest. There have been, however, reports of cultivars that appeared to be less damaged during severe natural infestations of germ-plasm and breeding lines (ICAR, 1969, 1971, 1972, 1974; Jotwani, Sukhani and Matai, 1971; Leuck *et al.*, 1968; Kalode and Pant, 1966; Sandhu, Luthra and Singh, 1976). Reliable screening techniques have been developed in maize and sorghum for identification of resistance to stem borers and shootfly (Jotwani and Davies, 1980) and these should be readily applicable to pearl millet. The task will probably be much more difficult for *Rhagava* resistance because, while little is known of the life history or biology of the pest, its unpredictable appearance and disappearance at different sites in different years are well known.

Parasitic weeds. Little work has been done on resistance to witchweed in pearl millet, though progress has been made in identification of resistance to *S. hermonthica* and *S. asiatica* in sorghum (Ramaiah, 1951; Vasudeva Rao, Chidley and House, 1982). The basic strategy has been to develop *Striga*-sick plots by incorporating large quantities of seed of the appropriate *Striga* spp. There is, however, a major problem in ensuring uniformity of challenge, because it is difficult to distribute witchweed seed uniformly throughout large screening areas, and soil heterogeneity provides different environmental conditions in different parts of the screening area during the critical period for infestation. The only way to overcome this problem is by sufficient replication, in space and time, and the use of frequent systematic susceptible checks. At the ICRISAT Centre, sorghum has been successfully screened for resistance to *S. asiatica* using three processes: (i) preliminary screening with one check for eight test plots; (ii) advanced screening with a check alongside each test plot; (iii) multiloational screening at known "hot spots" (Vasudeva Rao, Chidley and House, 1982).

A second major problem in screening for resistance to witchweed is just how to measure

susceptibility, particularly in genetically variable populations, and a great deal of research is needed to develop effective and relevant screening techniques for resistance to witchweed. Plant pathologists should be involved in such work because of the similarities in working with soilborne plant pathogens. At the present time there is a pitifully small research effort into the pearl millet witchweed problem in Sahelian Africa, and this must be vastly increased if progress is to be made in reducing the effects of this major yield constraint.

Sources of resistance

Diseases. Sources of disease resistance in pearl millet were reviewed by Williams (1983). Details are summarized below.

Downy mildew. Two major efforts have been made to screen the world pearl millet germ-plasm collection for resistance to downy mildew (Murty, Upadhyay and Manchanda, 1967; Williams, Singh and Thakur, 1982), under conditions of natural disease development and also latterly using uniform inoculation techniques (Williams, Singh and Pawar, 1981). In both studies the highest proportion of resistant accessions were identified in those from Africa. In the later study the central region of West Africa, particularly northern Nigeria, southern Niger, the Upper Volta and Mali, provided the richest sources of resistance. However, only a relatively small proportion of the more than 14 000-entry world germ-plasm collection has been effectively screened for downy mildew resistance, mainly because of the success obtained in developing sources of resistance from initially susceptible lines or populations through recurrent selection and, to a lesser extent, mutation breeding. There is a need, nevertheless, for a greater effort in classifying the downy mildew susceptibility/resistance of the remaining accessions in the world germ-plasm collection.

Irradiation of seed of susceptible lines is reported to have yielded new sources of resistance (Murty, 1973; Pokhrtyal and Jain, 1974;

Murty, 1974; Jain and Pokhriyal, 1975). A potentially valuable new male-sterile line derived from a selection programme at ICRISAT among progeny of irradiated susceptible lines (Kumar *et al.*, unpublished data) has been used to make several experimental hybrids, some of which have entered the Indian national evaluation programme. It will be several years, however, before the true value of this resistance source becomes apparent.

Levels of resistance to downy mildew in initially susceptible populations have been increased through a process of recurrent selection within populations while maintaining or improving other desirable and adaptive features of the population (ICRISAT, 1981; Williams, Singh and Thakur, 1982; Williams, 1983). One of the products of the ICRISAT Pearl Millet Improvement Programme's recurrent selection project has been released for cultivation by the national programme in India, after it had been shown to combine high yield stability and downy mildew resistance during several years of multilocational trials in the sub-continent.

Since 1976, the levels of downy mildew resistance in entries submitted to the hybrid and variety preliminary yield trials of the All India Coordinated Millet Improvement Programme have steadily increased, so that by 1981 almost all entries had no more than a ten percent incidence of downy mildew in screening trials at ICRISAT (Williams, 1983).

Ergot. In the 1960s and early 1970s attempts were made in India to locate sources of resistance to ergot, with little success (Kumararaj and Bhide, 1962; Shanmugasundaram *et al.*, 1968; ICAR, 1971; Pathak and Sharma, 1976b), primarily due to the lack of an efficient, reliable screening technique. In the mid-1970s the phenomenon of pollen interference in ergot infection was detected (Thakur and Williams, 1980), which had major implications for screening pearl millet for ergot resistance. The improved screening technique (Thakur, Williams and Rao, 1982), described above, was developed on the basis of this information and has been used to screen germ-plasm and breed-

ing materials since 1978. The authors quoted above have recently described the ICRISAT programme's successful efforts in developing ergot resistance. In the germ-plasm of the more than 4 000 entries screened no high level of ergot resistance was detected, although selection among the progeny of crosses between lines that were consistently relatively less susceptible yielded many lines that developed only low levels of ergot (<1 percent florets infected) by the F₆ generation.

Similar attempts to develop ergot-resistant selections have been made at other locations in India in the last few years (S.S. Chahal, personal communication; Harinarayana, 1982) utilizing the improved screening technique. However, the high ergot susceptibilities of the hybrids and varieties in the 1981 yield trials of the All India Coordinated Pearl Millet Improvement Programme (ICAR, 1982; Williams, 1983) indicate that the resistance has not yet been incorporated into high-yielding hybrids or varieties.

Smut. Prior to the late 1970s there were few reports of sources of resistance to smut in pearl millet. Murty, Upadhyay and Manchanda (1967) published a list of reactions to smut of 1 508 entries in the world collection, with indications that several accessions from Africa and India were possibly resistant. Pathak and Sharma (1976a) reported 11 of 322 lines of diverse origin to be relatively less susceptible to smut and Yadav (1974) reported six lines to be smut resistant. More recently, screening for sources of resistance to smut has become a major activity in the ICRISAT Pearl Millet Improvement Programme, with several hundred lines being screened each year and about 30 lines being evaluated annually in multilocational testing (ICRISAT, 1981). These reported sources of resistance, however, have not yet been successfully utilized in the development of improved varieties and hybrids, as witnessed by the high smut susceptibility of the entries in the various 1981 yield trials of the All India Coordinated Millet Improvement Programme in screening trials at ICRISAT (ICAR, 1982; Williams, 1983).

Rust. In the evaluation of 1 508 germ-plasm accessions by Murty, Upadhyay and Manchanda (1967), three lines were free from rust and 81 entries appeared to have low susceptibility (with a score of 2 as registered on a 1 to 5 scale). Other resistant lines have been reported in the literature (Ramakrishnan and Sundaram, 1956; Suresh, 1969). Screening and selection of world germ-plasm for rust resistance commenced at ICRISAT in 1975 and, although no artificial screening technique had been used, late planting at the ICRISAT Centre farm and at Bhavani Sagar in southern India allowed a reliable challenge of the test materials (Singh and Williams, 1978). More than 20 lines have been consistently resistant to rust in these trials (less than ten percent of the surface of the upper four leaves supporting rust pustules at the soft dough stage of seed maturity) (Singh and Williams, 1978).

Blast. Screening for sources of resistance to blast in pearl millet has been carried out at a few locations in northern India, on a relatively small scale, generally relying on natural infection with no inoculation. Sources of resistance reported in recent studies by Pathak *et al.* (1976), Duhan and Thakur (1980) and Yadav, Agnihotri and Prasada (1980) have been listed by Williams (1983).

Helminthosporium leafspot. Singh, Choudhary and Bhatnagar (1980) screened 118 pearl millet lines for resistance to *Helminthosporium rostratum* by inoculating seedlings with conidial suspensions of the pathogen. Eleven lines remained symptom free.

Curvularia leafspot. In the trials of Patil (1972) none of 108 test lines were free from disease caused by *Curvularia penniseti* var. *poonensis*. One line was highly resistant at the seedling stage and 13 lines showed adult plant resistance.

Multiple disease resistance. The lines being developed for ergot resistance at ICRISAT have been routinely screened for downy mildew and smut reactions, so that resistance to

these two diseases has also been developed in these lines (Williams, Singh and Thakur, 1982). The ergot, smut and downy mildew reactions of the five lines with the highest levels of ergot resistance in 1981 are presented in Table 3.

Insect pests and witchweed. Effective screening techniques have not yet been developed for identifying resistance to insect pests and witchweed in pearl millet. However, apparently less susceptibility has been reported to stem borer (Sandhu, Luthra and Singh, 1976), shootfly (ICAR, 1974) and *S. hermonthica* (Roger and Ramaiah, 1981). These apparent sources of resistance will need to be re-evaluated when reliable screening techniques have been developed.

Tests For stable disease resistance

Multilocal testing. If reliable disease-resistance screening techniques are used correctly on a rich, well-chosen germ-plasm collection, then it is probable that resistance to most diseases will be identified at the "home" location. However, the question remains as to whether this resistance will be effective when the varieties are grown in another region or another year, with possibly different pathogenic races and different levels of agro-climatic parameters, (i.e. is the resistance stable

TABLE 3. Sources of multiple disease resistance in pearl millet in India¹

Line	Mean ergot ² severity (%)	Smut ³ severity (%)	Downy mildew ⁴ incidence (%)
ICMPE 134-6-9	2	0	7
ICMPE 134-6-11	2	0	0
ICMPE 134-6-41	2	0	3
ICMPE 134-6-34	2	0	4
ICMPE 134-6-25	2	0	4
Susceptibility check	41	54	45

¹Source: Williams, Singh and Thakur, 1982. ²Based on the 1981 IPMEN results of 10 locations in India. ³Based on 20 inoculated heads during the 1981 rainy season at the ICRISAT Centre. ⁴Based on the ICRISAT Centre 1981 rainy season downy mildew nursery.

or unstable?). The most satisfactory way of answering this question is to subject the varieties to multilocal testing so that the resistance is evaluated against many populations of a particular pathogen under a wide range of environmental conditions. Test locations in the centres of origin and diversity of a crop are particularly valuable. If these are the centres where the host and pathogen have co-evolved over a long period, that is where the greatest range of pathogenicity can be expected.

The International Pearl Millet Disease Resistance Testing Programme (IPMDRTP)

In 1976 the International Pearl Millet Disease Resistance Testing Programme was initiated as a joint activity between scientists in national programmes and ICRISAT, to evaluate the stability of reported sources of disease resistance and to begin to examine the virulence of diverse populations of the pathogens of pearl millet. International nurseries have been distributed to cooperating scientists in several African and Asian countries annually for the purpose of identifying sources of stable resistance to downy mildew, ergot, smut and rust.

Downy mildew. Multilocal testing for downy mildew resistance in pearl millet has been conducted cooperatively with national programme staff in India and in several West African countries in two stages. In the first stage, a 150-entry Pre-International Pearl Millet Downy Mildew Nursery (Pre-IPMDMN) was tested at a few key downy mildew "hot-spot" locations in India and West Africa. The best entries from the Pre-IPMDMN in one year were moved forward into the full IPMDMN the following year for testing at many more locations. Some entries from West Africa have performed well across seasons and locations throughout the IPMDMN programme, although there have been occasional occurrences of more than ten percent downy mildew, generally in West Africa. The detailed results are available in the reports of the Pre-IPMDMN and IPMDMN, published annually

by ICRISAT. The evidence indicates that some West African lines multiplied for several generations at the ICRISAT Centre in India have lost the original high level of resistance experienced in West Africa.

Wide differences in the downy mildew severity values among locations have been observed for several entries, not only between India and Africa, but also among locations in West Africa. This indicated the probability of variation in pathogenicity among populations of *Sclerospora graminicola*. In 1978, therefore, an International Pearl Millet Downy Mildew Differential Trial (IPMDMDT) was initiated to examine the validity of the apparent differential reactions of entries in previous years and to identify potential differential hosts for further study of the pathogenic variability of this pathogen. The trial confirmed earlier results and provided clear indications that considerable pathogenic variability exists within the pearl millet-infecting pathotype of *S. graminicola*. The potential differential host cultivars identified are now being used for intensive investigations into pathogenic variability in *S. graminicola* at the University of Reading, UK, where initial studies have confirmed major differences in pathogenicity among isolates (Ball, 1983).

Ergot. The resistant lines identified from crosses among relatively less susceptible lines (Thakur, Williams and Rao, 1982) were tested at several locations in India and Nigeria in the 1981 International Pearl Millet Ergot Nursery (IPMEN). The most resistant entries at Indian locations in this trial were five lines from the cross J-2238 x J-2210-2. In Nigeria, however, these lines had much higher levels of ergot, and the best entry found there came from a cross between two Nigerian lines. Other lines that had little or no ergot at the ICRISAT Centre developed more ergot at certain Indian locations, the reasons for which require investigation. Progenies from other crosses are being developed in the ICRISAT ergot resistance development project, which should provide additional diversified ergot resistance sources in the near future.

Smut. The International Pearl Millet Smut Nursery (IPMSN) was initiated in 1975 and testing has been performed annually. Some entries have shown consistent resistance to smut in India and in some locations in West Africa (Williams, Singh and Thakur, 1982).

Rust. The lines identified as resistant in the ICRISAT screening programme (Singh and Williams, 1975) have been tested annually at several locations in India through a cooperative testing network in the International Pearl Millet Rust Nursery (IPMRN), which was first initiated in 1977. Eight entries have given resistant reactions at several locations in tests conducted over a period of two to three years (Williams, 1983). More work is needed on resistance to this disease, with an evaluation of the variation in parameters that will contribute to slow development of esodemics.

Utilization of disease resistance

Two main breeding approaches are possible in pearl millet: (i) recurrent selection in breeding populations (often termed composites), which are operated with a minimum amount of inbreeding (S_1 progeny testing has been found to be the most effective method, though also the most resource consuming); and (ii) the conventional pedigree system where variability generated in variety crosses (or by mutation) is separated into discrete lines by inbreeding. These two methods have different consequences for the nature of the genetic resistance most likely to be retained after selection. Two types of end product are used commercially: varieties (including traditional landrace varieties) and single-cross hybrids. These also have consequences as to the type of genetic control of resistance that can be most easily utilized.

A variety may be defined as an inter-mating population in equilibrium, which is the natural genetic state for pearl millet, and for a given pathogen it can contain a number of resistance genes, both major and minor, and being duplicate or additive in effect. Dominant or partially dominant resistances are easiest to manipulate

in variety populations. New varieties, if developed without serious levels of inbreeding, will contain all the genes present in the original population but in different frequencies, depending on the selection pressures applied. This has two effects: (i) varieties are unlikely to show total resistance to a given population of a pathogen (but the level of resistance expressed may be totally effective in providing economic control); and (ii) the residual variation for resistance can permit the variety population to be reselected for resistance to a new pathogen or other disease.

Single-cross hybrids are an artificial state for a cross-breeding species such as pearl millet, and the history of grain hybrids in India since 1965 bears testimony to their vulnerability to disease and relatively short life expectancy. The positive aspect of this history, however, is that, although in use for only five years, hybrid HB3 contributed food worth thousands of millions of rupees, and so has its replacement BJ104. This raises a question, of fundamental consideration to all breeders working with genetic resistance to pests and diseases, of how much resistance is required for economic protection. Incorporating resistance to pests and diseases is only one necessary aspect in the breeding of new varieties or hybrids with improved yield and quality. There is a view that incorporating excessive levels of disease resistance, which are out of proportion to the expected life of the hybrid in respect to its other attributes, amounts to over-kill and a waste of valuable research resources. The Indian hybrid HB3 is cited as evidence supporting this point. However, had it not been for the downy mildew susceptibility of HB3 it would probably still be grown today, as the yield levels of the currently used hybrids are in no way superior. Thus, the converse view can also be supported, that if HB3 had possessed stable and durable downy mildew resistance, the massive use of resources to find replacements would not have been needed. Breeders have found that using one resistant parent in hybrid combination is often sufficient to confer resistance in single-cross hybrids. It remains to be determined whether this is a wise practice or whether the presence of

resistance in both parents will provide more durable resistance. There is a debatable view held by many breeders that commercial single-cross hybrids in pearl millet will need to be replaced every five years or so, for as progress is made in breeding this is likely to happen for reasons of yield and quality as well as for changes in disease susceptibility.

Downy mildew. Identifying, distributing and utilizing stable downy mildew resistance has been a major goal of the ICRISAT Pearl Millet Improvement Programme from its inception in 1973. While sources of resistance have been identified that were effective in both India and West Africa, it has become apparent that, during the utilization of such sources in India, resistance to downy mildew in West Africa has been progressively reduced. A good example is provided by the World Composite (WC) from Nigeria where it exhibited good resistance to downy mildew (and other diseases); after selection in the ICRISAT downy mildew nursery for several generations, this composite and varieties made from it continued to show excellent resistance to downy mildew in India, but they showed deteriorating levels of resistance when tested in Nigeria. The overall conclusion has been that selection for downy mildew resistance for West Africa has to be conducted there. Crosses between lines from India and Africa are sent as F_1 s or F_2 s for selection in the region of Africa where they are to be utilized. Though most material from Africa is resistant to downy mildew in India, it is unadapted in other ways (excessive lateness and unbalanced tillering) and thus needs reselection in India.

Both breeding approaches in pearl millet, as described previously, have been used in the ICRISAT programme to breed for yield and downy mildew resistance. This programme has put slightly more effort into breeding varieties rather than hybrid parents for two reasons: first, the greater part of the national effort in millet improvement in India was already directed toward hybrid development; second, stable resistance to downy mildew was easier to obtain in improved varieties, which also have higher levels of resistance to ergot and smut.

Also, variety development work has greater relevance to African needs.

During the formation of the ICRISAT base composites in 1973-74, care was taken to include parents of Nigerian origin, which conferred good resistance to downy mildew because of their origin. Other composites were derived from breeders' populations from the Niger, the Upper Volta, Senegal and Uganda. Of these, populations from Senegal and Uganda initially contained insufficient resistance to downy mildew in India, but this was rapidly increased through reselection in the ICRISAT downy mildew nursery (Williams, 1983). In order to select for increased downy mildew resistance in composites, the material is exposed twice during each selection cycle. During the progeny testing phase one replication is grown in the downy mildew nursery and the best plants selfed in all progenies. Seed from these plants (not remnant seed) is used to represent the selected progenies in the recombination generation, which is also grown in the downy mildew nursery. Only disease-free plants are used in recombination. This process permits selection for downy mildew resistance between and within progenies during the testing phase and again during the recombination stage within the selected progenies, which, because they were previously selfed, continue to segregate for resistance/susceptibility.

The purpose of deriving partial and complete inbreds from variety crosses is to: (i) identify annually sets of useful lines from the F_3 to F_5 generations for distribution to cooperators as a routine supply of new variability; (ii) use them as parents to make synthetics; (iii) test them for use as hybrid parents. Each of these objectives requires that the lines be screened for downy mildew resistance, once or twice for objectives (i) and (ii) but repeatedly for objective (iii). It is in this last case, where lines show that they are potential male-sterile maintainers, that the downy mildew nursery is most intensively used during breeding, since all the generations of selection and backcrossing, up to the fifth or sixth backcross, are grown exclusively in the downy mildew nursery. During the development of several new male-sterile lines and

TABLE 4. Summary of ergot reactions of test crosses using ergot-resistant (ER) F₅ lines on three male-sterile (ms) lines during the 1980 rainy season¹

ms lines	No of F ₁ hybrids	Mean ergot severity (%)(2,3)		
		mg lines	ER F ₅ lines	F ₁ hybrids
111A	189	76	<1-20	63-8S
5054A	216	80	<1-20	84-9S
5141A	237	83	<1-20	65-92

¹Source: R.P. Thakur *et al.*, unpublished data. - ²Mean of 10-30 inoculated heads. - ³Ergot severity range of 30 ER F₅ lines used in test crosses.

evaluation of existing male-sterile lines and their isogenic maintainers, evidence was gathered to show that the Al cytoplasm (as carried by Tift 23A, the female parent of HB3) does not contribute to downy mildew susceptibility (Kumar *et al.*, unpublished data).

Ergot. Ergot is prevalent in both India and Africa, though the pollen-interference phenomenon is usually sufficient to provide protection in varieties. However, heavy ergot attacks can be induced in varieties by unusually humid weather conditions, abnormal sowing (and hence flowering) dates or the presence of some earlier-flowering susceptible genotype (such as a hybrid). Hybrids produced using cytoplasmic male sterility are generally highly susceptible to ergot, and it is in these that resistance is urgently needed. Conditions for ergot attack seem to be more favourable in many African countries, and it may not be possible to use hybrids there for this reason until effective levels of resistance to ergot are bred into hybrid parents.

The work required to generate ergot-resistant lines and the results of crosses between these lines and susceptible seed parents provide evidence on the inheritance of ergot resistance and how it should be utilized. The fact that high levels of resistance could not be found in any germ-plasm source and could only be obtained from crosses between lines with moderate resistance indicates involvement of several genes. Crosses between ergot-resistant lines and susceptible male-sterile lines have given totally susceptible hybrids (see Table 4), indicating

that resistance is recessive and/or possibly that male-sterile cytoplasm is connected with susceptibility. Crosses between different lines with high levels of ergot resistance produced F₁ generations that were not all as resistant as the parents, indicating that resistance is controlled by at least several genes with additive effects. Similarly, synthetics made from intercrossing several sources of resistance showed moderate resistance, and the inclusion of any susceptible parent lines suppressed resistance (see Table 5). The implication is that to obtain ergot-resistant hybrids, resistance, preferably from the same source, will be needed in both parents of the hybrid. A project to achieve this has been initiated at ICRISAT, using two common male-sterile lines and several desirable pollen parents. The ergot-resistant synthetics can probably be improved rapidly, both for yield and resistance, through the use of an ergot-resistant inbred tester.

Crosses made to compare the effects of cytoplasm on ergot susceptibility provide some indication that male-sterile cytoplasm may be associated with susceptibility, but this observation needs further testing.

Smut. The fact that lines with high levels of resistance have been obtained from a range of backgrounds, including breeding material, by selfing and selecting under disease pressure is

TABLE 5. Ergot reactions of three synthetics made from ergot-resistant F₅ lines and one from a mixture of ergot-resistant and susceptible lines¹

Synthetic(x) ²	Ergot severity (%) ³	
	Mean	Range
ICMS 8031 (5)	12	5-30
ICMS 8032 (6)	15	5-40
ICMS 8034 (5)	14	5-35
ICMS 8102 (5) ⁴	50	1-100
WC-C75 (variety check)	24	10-50
BJ-104 (hybrid check)	54	25-80

¹Source: R.P. Thakur and S.B. Chavan, unpublished data. - ²Number of lines used in constituting the synthetics. - ³Mean of 10-20 open inoculated heads. - ⁴Synthetic made from two ergot-resistant and three susceptible lines.

promising for the prospects of utilization. In susceptible \times resistant test crosses a range of susceptibilities occurred, indicating that resistance may be partially dominant (for highly resistant hybrids, however, it is likely that both parents will need good levels of resistance), and crosses between resistant lines are highly resistant.

The recovery of smut resistance in progenies of crosses between agronomically elite, but susceptible, lines and smut-resistant parents has proved relatively easy compared with ergot, and by the F_5 generation more than 50 percent of the lines retained after selecting under inoculation in the F_2 to F_4 generations recorded smut severities of less than 10 percent (see Table 6).

In the process of crossing smut resistance into a B line, 30 F_4 progenies derived from the initial cross between the B line and the smut resistance source were test crossed on to an A line. Of the test crosses, 14 were male-fertile and 16 were male-sterile. The members of the male-sterile group were statistically more susceptible than the male-fertile group (see Table 7), indicating that pollination reduces smut severity.

Since good smut resistance had been identified from a variety of backgrounds, a smut-resistant composite (SRC) was formed in 1978 using 37 low-susceptible parents. When 562 half-sib progeny were tested in 1980, nearly 80 percent were found to have smut severities of less than 10 percent. From the best 117 half-sib

TABLE 7. Male sterility and smut severity (%) in 30 test crosses on MS-81A using F_4 sister lines as pollinators¹

Test cross status	Mean ²	Range	F ratio (transformed data)
Fertile (n = 14)	33.6	16-62	34.34
Sterile (n = 16)	47.6	10-S8	

¹Source: K. Anand and R.P. Thakur, unpublished data. ²Based on 10 inoculated, bagged heads. * Indicates statistical significance at $p < 0.05$.

families, 244 S_2 lines were extracted and more than 50 percent of these had less than 1 percent smut when tested at Hissar in 1981. The 54 best have been recombined to form the C1 bulk, which represents the basis of a further cycle of selection for yield and for resistance to downy mildew and smut.

Multiple disease resistance. Large-scale screening for resistance to downy mildew, ergot and smut can be operated on the same plants by using the several screening techniques that have been developed. Only those lines showing acceptable levels of downy mildew resistance, which can be assessed by the time of flowering, are inoculated with the ergot and smut pathogens. Sources of downy mildew plus ergot resistance and downy mildew plus smut resistance have already been found, and several closely related lines have been identified with resistance to all three diseases (see Table 3). A disease-resistant composite will be formed when parents with sufficient genetic diversity and each carrying multiple resistance have been identified.

Shibras. Shibra gene contamination can be eliminated by a process of inbreeding for one generation, evaluating S_1 progeny, and recombining only the best 25 to 50 of these, which show no shibras, using remnant seed. This process has a double benefit as it permits positive selection to be made for other traits, particularly yield and downy mildew resistance. The number of S_1 progeny to be tested should be at

TABLE 6. Smut reactions of 95 F_6 progeny derived from a cross between smut-susceptible and smut-resistant parents¹

Smut severity (%) class*	No. of progeny	Frequency
0-10	50	53
11-20	13	14
21-30	14	15
31-40	6	6
41-50	7	7
51-60	3	3
61-70	1	1
71-80	1	1

¹Source: R.P. Thakur and K.N. Rai unpublished data. * Mean of 10 inoculated, bagged heads.

least 500, preferably in two replications, but plots need not have more than about 50 plants each. These S_1 progeny are best obtained by selecting at least 800 superior heads from several well-grown fields of the variety to be improved. These are grown in the off-season in very small plots (five to ten plants per plot) and two or three typical plants are selfed in each plot. At harvest, the single best plant from each plot is selected, and some plots may be rejected entirely. After evaluation of the S_1 progeny, the recombination of the 25-50 selected S_1 plants using remnant seed must be done in the off-season to avoid the process of recontamination from other farms and from wild species.

Prospects for achieving durable disease resistance

Stable resistance can be identified through the process of multilocational testing. Unfortunately, there is no necessary correlation between stable resistance and durable resistance. The only certain way to identify durable resistance is to grow a cultivar commercially on a large scale over a long period. There are, however, certain features of the host pathogen and pathosystem that enable some degree of prediction of the possible durability of resistance.

When a strong specific selection pressure is exerted on a genetically variable population, the population moves in the direction of the selection pressure. The introduction of a disease-resistant cultivar can exert a strong selection pressure on a pathogen population. Thus, when considering the likely durability of a new resistant cultivar, knowledge is needed as to the strength and specificity of the selection pressure, the variability of the pathogen and the survival and dispersal capabilities of novel pathogen genotypes.

Selection pressure. A resistance mechanism conferred by the action of a single gene, which precludes the development of a pathogen during or immediately following initial penetration, provides the strongest and most specific selection pressure on a pathogen population.

Resistance conferred by the additive action of several genes, which retard the several processes of infection, colonization and the capacity to sporulate, provides a much weaker and less specific selection pressure. Thus, when used against a highly variable pathogen population, single immunity genes are unlikely to be durable. Rather, they will be liable to sudden "breakdown". Conversely, resistance conferred by the additive action of several genes that control several aspects of pathogen development and dispersal will not be subject to sudden "breakdown", and thus is more likely to be durable but may erode gradually over a long period.

Pathogen variability. Mutations to overcome specific resistance genes occur at random at a certain low frequency in pathogen populations. As the production of infective propagules increases, the probability of a propagule that possesses the required virulence gene encountering a resistant plant on which it will be selected also increases. Where combinations of several resistance genes confront the pathogen, its capacity for genetic recombination will be an important determinant of the speed of response to the selection pressure of the host resistance.

Survival and dispersal of novel pathogen genotypes. The epidemiology of a disease has important implications for the survival and dispersal of novel pathogen genotypes and thus for the potential durability of resistance. Where there is a distinct non-crop off-season, and the propagules that initiate crop infection each year come from a wild host reservoir, or where the initial inoculum blows in from a distant location with an earlier crop season and different varieties, there will be a low survival potential for pathotypes that are selected on the crop. Where the inoculum for one year's crop is provided by resting bodies or dormant mycelium in debris from the previous year's crop, then the probability for survival of novel pathogen genotypes is higher. The novel genotypes of a pathogen that produces vast numbers of airborne propagules will be much more rapidly dispersed than those of a pathogen that is soil-borne and soil-transmitted.

It is apparent that, in order to predict and develop strategies to extend the durability of resistance of a particular host to a particular disease, a thorough knowledge is required of the nature and genetics of the resistance, the variability potential of the pathogen and the epidemiology of the disease in the particular epidemiological unit in which the resistant cultivar is to be commercially used.

The biology of the four major pathogens of pearl millet, *S. graminicola*, *C. fusiformis*, *T. penicillariae* and *P. penniseti*, indicates their probable ability to be able to respond rapidly to specific strong selection pressures (Nene and Singh, 1976; Singh and Williams, 1980; Williams, 1983, 1984; Michelmore, Pawar and Williams, 1982). Thus, the nature and genetics of cultivar resistance are likely to be important determinants of resistance durability.

Nature and genetics of resistance

Although penniseta are hermaphroditic, they show pronounced protogyny, which leads to a normally high level of cross-pollination (Rachic and Majmudar, 1980). Thus, in landrace cultivars, in which there is random cross-pollination, considerable genetic variability can occur among the plants that constitute a cultivar. This variability probably enables the crop to reduce the effects of specific stress factors, including plant pathogens (e.g. when considering a cultivar with five major-effect resistance genes, these five genes can occur in 31 different combinations after several generations of random mating, with the effect that the cultivar behaves as a naturally occurring multiline).

F₁ hybrids, which are produced primarily through the crossing of two inbred lines, have reduced heterogeneity, which makes the hybrids more vulnerable to disease epidemics than composite cultivars. The use of pollen from a heterogeneous population to create an F₁ hybrid would probably be less likely to create a disease-vulnerable hybrid than the use of an inbred line as the male parent.

A recently suggested strategy (ICAR, 1982) is to use hybrid blends or mixtures to combine

the yield advantage of the hybrids with the greater stress resistance shown by more heterogeneous composite cultivars. A thorough knowledge of the genetics of resistance will be needed for this strategy to be utilized efficiently.

Downy mildew. Although it appears that "partial resistance" to downy mildew is the norm in pearl millet (because it is unusual to find test lines completely free from the disease), this does not necessarily mean that resistance is polygenic in individual plants as may be the case with a rust of a self-pollinated cereal. Because of the outcrossing nature of the crop and the systemic nature of the pathogen, individual plants are generally scored on a qualitative basis (they are either diseased or they are not), whereas the score for the whole line is given as a quantitative score. Thus, 10 percent incidence does not mean that all plants were diseased with an average disease score of 10 percent; it means instead that out of 100 plants 90 were free from disease and only 10 were diseased. The 90 disease-free plants may all possess the same single immunity gene, or there may be several combinations of different immunity genes, and/or they may possess several additive genes that slow down the pathogen so much that disease does not develop. If the durability of resistance is to be assessed, it must be known which of these situations is acting for any resistant cultivar. The authors are not aware of any critical histopathological studies on the nature of resistance of downy mildew in any pearl millet cultivar. There are, however, several reports of studies on the inheritance of resistance (Appadurai, Parambaramani and Natarajan, 1975; Gill et al., 1975, 1978; Pethani, Kapoor and Chandra, 1980) with somewhat conflicting and unclear results. This probably reflects the difficulties that exist in attempting to study inheritance of resistance in host cultivars of an outcrossing crop, when such cultivars are generally neither completely resistant nor completely susceptible when inoculation techniques that are less than 100 percent effective are used with pathogen populations undefined for pathogenicity. If inheri-

tance studies are to provide meaningful results, ways must be found to ensure that the plants used in the crosses are definitely resistant or susceptible (susceptible diseased plants could be cured by treatment with metalaxyl fungicides), inoculation procedures must be standardized and the isolates of the pathogen should be defined and maintained in the asexual state.

There is no doubt that if durable resistance is to be developed, particularly through the strategy of hybrid blends, genes for resistance will need to be identified and manipulated. The recent recognition of a type of susceptibility that prevents the development of esodemics (Williams, Pawar and Singh, 1982) highlights the need to consider the type of susceptibility exhibited by test materials when an exodemic system of screening is employed.

Ergot. Until very recently there were no reliable sources of resistance to ergot in pearl millet, and thus there are no reports of specific studies on the nature and inheritance of ergot resistance in this crop. However, quantitative reactions in this disease are obtained on an individual plant basis, so that one percent disease could indicate that all plants were diseased and that the average severity per plant was one percent. Thus, with ergot, it is unlikely that immunity genes are involved. In addition, Thakur, Williams and Rao (1982) concluded that resistance to ergot is recessive and polygenically controlled, on the basis of results obtained while developing resistant lines. Such resistance could be highly effective and would be expected to be durable in F_1 hybrids, provided the resistance genes are manipulated into both the male and female parents.

Smut. In the only paper found on the inheritance of smut resistance in pearl millet, Yadav (1974) concluded that resistance was controlled by either single- or double-gene action. This equivocal conclusion is probably the result of non-uniformity in reaction of the parental material similar to that referred to in the section on inheritance of resistance to downy mildew. Now that new stable sources of smut resistance

have been identified, further work is needed on the nature and genetics of resistance to this disease, but the parent plants used must be truly resistant and susceptible, and effective standardized inoculation techniques must be used.

The occurrence of quantitative differences in susceptibility on an individual plant basis and evidence of the manner in which resistance levels can be raised within test lines suggest that smut resistance is polygenically controlled. Research is needed to test this hypothesis.

Rust. Observations of the rust reactions of a large number of pearl millet germ-plasm lines in southern India (R.J. Williams, unpublished data) indicated that several resistance mechanisms probably occur. Large differences in pustule intensity and pustule size and appearance were seen and necrotic flecking, characteristic of hypersensitive reactions, was also observed. A great deal of careful research is needed both to substantiate these hypotheses and to utilize the most appropriate characters in a disease resistance breeding programme.

Priorities for future research

Pearl millet has a rich and diverse germ-plasm which the authors firmly believe contains all the resistance genes needed to breed pest- and disease-resistant cultivars in this crop. Germ-plasm has to be collected and evaluated in an intelligently directed manner, utilizing accessions from regions where high selection pressures for the necessary characters are likely to have occurred. The breeding system of pearl millet and its relatively short duration indicate that rapid advances can be made in breeding.

For diseases, the major work needed is in evaluation of the nature and inheritance of the identified resistances, and this knowledge must be used in the development of strategies to increase resistance durability. The possibility of presenting complex multiple barriers to pathogens (e.g. the combination of polygenic resistance and systemic seed-applied fungicides for downy mildew control) requires investigation.

For insect pests, additional survey work must be undertaken and major research conducted on the development and use of effective, meaningful resistance screening techniques. There will be a need for a clear understanding of the bionomics of the important insect pests and the evaluation of integrated control strategies using combinations of host-plant resistance, cultural control methods and possibly pesticide sprays, dusts and granules.

For witchweed, the most important research area concerns the development of a reliable resistance screening technique and its use to identify and develop witch weed-resistant cultivars.

A solution to the shibra problem in Sahelian Africa should be pursued by a combination of cultural practices and plant breeding.

In Africa it is important that pearl millet improvement programmes utilize the locally resistant cultivars as the basis for crop improvement, since exotic, so-called elite, improved millets developed in India or the United States are generally highly susceptible in Africa to the local strains of pathogens and pests, particularly in parts of West Africa. Flowering time, as determined by planting date, genotype maturity class and/or degree of photoperiod sensitivity, is a critical factor in the severity of inflorescence pests and diseases.

Regional research needs. It is apparent from the references cited in this article that most of the published research on pearl millet diseases and pests has been carried out in India. The crop, however, is grown on a larger area in Africa than in India and the germ-plasm in West Africa appears to be a richer source of disease resistance than germ-plasm collected in India. There are indications that the populations of the pathogens in West Africa are more

virulent than those in India and the insect pests, weed and bird problems in Africa are different from those found in India. This all points to the fact that much more research is needed on pearl millet diseases and pests in Africa. The establishment of the ICRISAT Sahelian Centre near Niamey is a step in the right direction, but rapid significant progress is unlikely to occur unless the diseases and pests of this crop are studied by well-qualified staff within national programmes. Training and motivation of local scientists to work on the diseases and pests of pearl millet are obviously high priority needs. A network of cooperating centres should be set up to identify and utilize host-plant resistance in the African continent. They should be staffed by well-trained plant pathologists, entomologists and plant breeders, who will need to be provided with the necessary resources to screen for and utilize sources of disease and pest resistance effectively.

In India, although a considerable effort is directed toward research on pearl millet diseases, the resources provided are often less than adequate. The research centres selected to carry out reliable resistance screening must be provided with staff that is not frequently changed, irrigation equipment that will not be dependent on erratic rainfall, and a plentiful supply of materials, such as selfing-bags marking pens, seed storage boxes, fuel for water pumps and vehicles, and so on.

The stage is set for rapid advances in the ability to control pearl millet diseases and pests through the use of host-plant resistance. The pace at which progress will be made depends on the human and material resources that national programmes devote to the research areas highlighted in this review and the degree of cooperative activities among national programmes.

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