Downy Mildew Disease of Pearl Millet

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Abstract

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Downy mildew (*Sclerospora graminicola*) is the most important disease of pearl millet (*Pennisetum glaucum*). It often results in almost total loss of grain yield due to complete or partial conversion of florets to leafy structures instead of grain ('green ear'). Although the disease is present in many countries of the world, it is particularly important in western Africa, and in India, where it has caused several severe and widespread epidemics and is a major threat to the cultivation of F_1 hybrids. Considerable progress, reported in this bulletin, has been made in understanding pathogen biology and disease epidemiology. This has led to the development of effective and reliable laboratory/greenhouse and field-screening techniques, identification of resistant sources, and use of resistance in breeding programs to develop resistant cultivars. Alternative control measures, particularly with fungicides, have been developed.

Resumé

Le mildiou du mil. Le mildiou (*Sclerospora graminicola*) est la plus grave des maladies du mil (*Pennisetum glaucum*). Il peut souvent détruire la quasi-totalité du rendement en grain. Les fleurs des plants infectés peuvent être complètement ou partiellement transformées en organes foliacés au lieu de grains (le symptôme de "l'épi vert"). Bien que le mildiou du mil sévisse dans plusiurs pays, il est particulièrement important en Afrique de l'Ouest, et en Inde, où il a souvent atteint des niveaux épidémiques et a constitué une principale contrainte à la culture des hybrides F_1. L'ouvrage rend compte du progrès sensible fait dans l'étude de la biologie de l'agent pathogène et de l'épidémiologie de la maladie. Cet avancement a permis la mise au point des techniques de criblage efficaces et fiables conçues pour être utilisées au laboratoire, en serre et en champ; l'identification des sources résistantes; et l'utilisation de la résistance aux programmes de sélection afin de créer des cultivars résistants. D'autres méthodes de lutte, surtout avec des fongicides, ont été également élaborées.

Resumen

Mildiú en el cultivo de mijo. Le mildiú (*Sclerospora graminicola*) es la enfermedad más importante que afecta el cultivo de mijo (*Pennisetum glaucum*). Resulta en la pérdida caci total de la rendición de granos a causa de la conversión completa o parcial de las florecillas a una espigas hojosas en vez de granos. Aunque dicha enfermedad se halla en varios países del mundo, es mucho más grave en caso de la Africa del Oeste, y India, donde ha causado epidemias severas y muy extendidas y constituye una amenaza enorme a la cultivación de híbridos F_1. Como señala este boletín, se ha hecho bastante progreso en el campo de bidogía patogénica así como en la epidemiología de enfermedades. Esto ha facilitado el desenvolvimiento de técnicas eficaces y seguras tanto en el laboratorio o en el invernáculo como en el campo, la identificación de fuentes resistentes y el uso de resistencia en programas de crianza a fin de desenvolver cultivares resistentes. Se han elaborado medidas alternativas de control, particularmente en lo que concierne a las fungicidas.

Cover: An aerial view of a downy mildew field-screening nursery at ICRISAT Center, showing the tall infector rows, and the test material in between. Inset: Disease-free (left) and malformed earheads (green ear, right).

Downy Mildew Disease of Pearl Millet

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International Crops Research Institute for the Semi-Arid Tropics
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Contents

Preface

Downy mildew remains a major biotic constraint to pearl millet production, particularly in India and western Africa. The first major epidemic in India occurred in 1971–72. Since then, many severe epidemics have caused major yield losses, particularly in F_1 hybrid cultivars. Control of downy mildew in pearl millet is a strategic priority for Indian agriculture. While downy mildew epidemics of this intensity are not known in western Africa, yield losses up to 50% have been reported, and management of the disease is a priority research objective.

Intensive research on pearl millet downy mildew has been conducted by scientists at ICRISAT and in a number of national programs during the last three decades. Significant advances have been made in understanding the biology of the pathogen, and the epidemiology of the disease, and in developing artificial screening techniques, identifying sources of resistance, breeding for disease resistance, and developing alternative control measures.

This bulletin has been prepared to communicate the current status of knowledge on downy mildew and its management to a wide range of research and extension personnel. It is intended to be comprehensive, and is particularly targeted to workers who have limited experience with and exposure to the disease, and who do not have ready access to research literature. The bibliography includes scientific journal papers and books which can be consulted for in-depth technical information.

Dr Josef Werder, one of the authors, passed away on 24 June 1992. He was the Principal Millet Pathologist at the ICRISAT Sahelian Center, Niamey, Niger, from February 1985. He made significant contributions towards the understanding of the downy mildew disease in western Africa, and will be sorely missed as a colleague and friend. This bulletin will contribute to his professional memorial.

D. E. Byth

Introduction

Downy mildew of pearl millet (*Pennisetum glaucum* (L.) R. Br.), sometimes referred to as 'green ear' disease, is caused by *Sclerospora graminicola* (Sacc.) Schroet.), which is the type species of the genus. It is the most widespread and destructive disease of pearl millet in India and western Africa (Rachie and Majmudar 1980). Pearl millet is grown for grain and forage on about 26 million ha in the tropical and subtropical areas of Africa and the Indian subcontinent (FAO 1983). The disease, first reported in India (Butler 1907), is present in more than 20 countries (Safeeulla 1976), and is a major factor limiting the full exploitation of the high yield potential of hybrids in India. Grain yield losses of 10–60% have been reported in various countries in Asia and Africa (Nene and Singh 1976). In India, downy mildew epidemics caused substantial yield losses in F_1 hybrids during 1970–76 (Safeeulla 1977), during 1983 and 1984, and again in 1987 and 1988.

Although downy mildew has been recognized as a potentially important disease of pearl millet since the early part of the 20th century, it attracted relatively little attention until the late 1960s. Since then, progress has been made in understanding the biology of the pathogen, epidemiology of the disease, and its control. However, the disease continues to be a major problem. This bulletin is intended to present a broad range of information about downy mildew of pearl millet in a manner that will be useful to researchers, extension workers, students, and farmers.

Geographical Distribution

Sclerospora graminicola is widely distributed in the temperate and tropical areas of the world, and is especially important in India (Nene and Singh 1976) and Africa (N'Doye et al. 1986, Chevaugeon 1952, Saccas 1954, Bouriquet 1963). In India, the pathogen is present in all the states where pearl millet is cultivated. It has, however, not been reported to have been found on pearl millet in the western hemisphere. The geographical distribution of *S. graminicola* is presented in Figure 1, and Table 1.

Economic Importance

A comprehensive data set for grain yield loss in pearl millet due to this pathogen is not available. Some reports suggest 6% loss in east China (Porter 1926), 45% in Allahabad, India (Mitter and Tandon 1930), and up to 27% loss from 1962 to 1964 in Rajasthan state, India (Mathur and Dalela 1971). According to reports from Africa, there was 60% loss in Mozambique (DeCarvalho 1949), 10% in Nigeria (King and Webster 1970), and 0–50% in other western African countries (CILSS 1986, CILSS 1987, Selvaraj 1979, Saccas 1954). The actual yield-reducing potential of downy mildew is high, and this was dramatically demonstrated in HB 3, a popular hybrid in India, when pearl millet grain production was reduced from 8 million t in 1970–71 to 5.3 million t in 1971–72 (AICMIP 1972) (Fig. 2). This reduction was, to a large extent, due to a downy mildew epidemic, in which yields in some fields were reduced by 60–70%. Subsequent to this epidemic, grain yield losses continue to occur quite frequently due to downy mildew epidemics in India (Singh et al. 1987). It has been demonstrated that the losses in yield can be directly proportional to disease severity (Williams and Singh 1981).

Symptoms

There is considerable variation in the symptoms, which almost always develop as a result of systemic infection. Systemic symptoms generally appear on the second leaf, and once these appear, all the subsequent leaves and panicles also develop symptoms, except in cases of recovery resistance where plants outgrow the disease (Singh and King 1988). The disease can appear on the first leaf also, under

Table 1. Report of the occurrence of *Sclerospora graminicola* on millets from different parts of the world[1].

Continent	Country	Author(s)	Year
Africa	Chad[2]	Saccas, A.M.	1955
	Egypt[3]	El-Helaly, A.F., Ibrahim, I.A., Assawah, M.W., Elarosi, H.M., Abou-El-Daheb, M.K., Michail, S.H., and Abd-El-Rahim, M.A.	1965
	Gambia[2]	Line, C.W.	1927
	Ghana[3]	Melhus, I.E., Van Haltern, F.H., and Bliss, D.E.	1928
	Malawi[2]	Annual Report of the Department of Agriculture, Nysaland, 1960/61	1963
	Mozambique[2]	De Carvalho, T.,	1949
	Niger[2]	Chevaugeon, J.,	1953
	Nigeria[2]	West, J.	1938
	Zimbabwe[2]	Whiteside, J.O.	1966
	Senegal[2]	Fourneau, L.	1929
	South Africa[3]	Departmental activities Botany—Journal of the Department of Agriculture, South Africa	1923
	Sudan[2]	Tarr, S.A.J.,	1957
	Tanzania[2]	Ritchie, A.H.	1927
	Burkina Faso[2]	Delassues, M.,	1965
Asia	China[3]	Takasugi, H., and Akaishi, Y.,	1934
	China (Northeast)[3]	Pai, C.K.	1958
	India[2]	Butler, E.J., and Bisby, G.K.	1907
	Iran[3]	Viennot-Bourgin, G.	1959
	Israel	Kenneth, R.	1966
	Japan[3]	Tasugi, H.,	1933
	Pakistan[2]	Ali, S.B.	1960
	USSR[3]	Zaprometoff, N.G.	1927
Australia and Oceania	Fiji[3]	Blackie, W.J.	1948
Europe	Bulgaria[3]	Savoff, C.	1929
	Czechoslovakia[3]	Picbauer, R.	1938
	France[3]	Kuhnholtz-Lordat, G., and Blanchet, G.	1949
	Hungary[3]	Moesz, G.,	1939
	Italy[3]	Moriondo, F.,	1958
	Netherlands[3]	Van Poeteren, N.	1934
	Rumania[3]	Savulescu, T., and Savulescu, olga	1955
	Spain[3]	Losa Espaha, T.M.	1955
	Southern Russia[3]	Borghardt, A.I.	1933
North America	United States[3]	Farlow	1884

1. Review of Applied Mycology.
2. Reported on pearl millet.
3. Reported on other millets.

Note: The list includes those countries where the presence of *Sclerospora graminicola* has been ascertained.

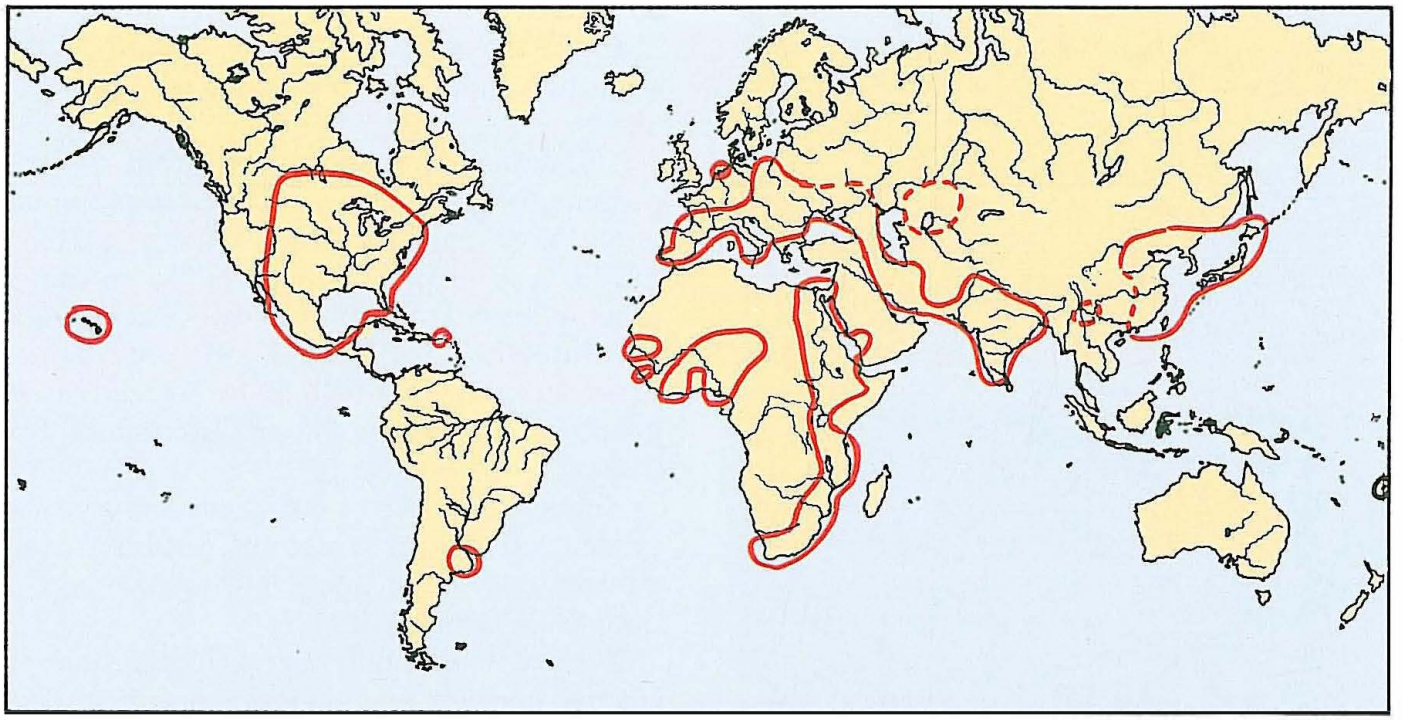

Figure 1. Geographical distribution of *Sclerospora graminicola* on different millets in the world. Source: CAB 1979.

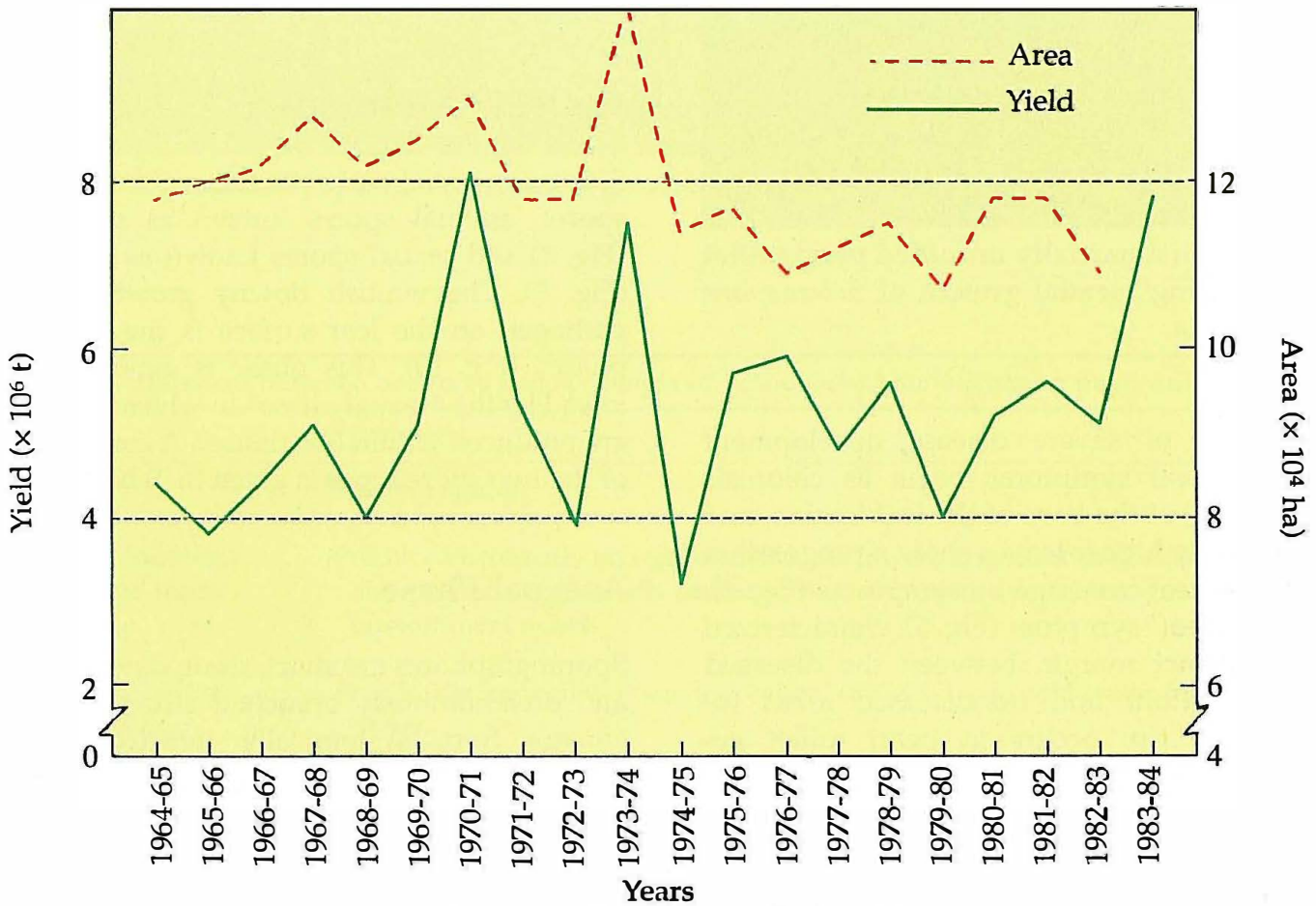

Figure 2. Area and production of pearl millet in India during 1965–84.
Source: Agricultural Situation in India.

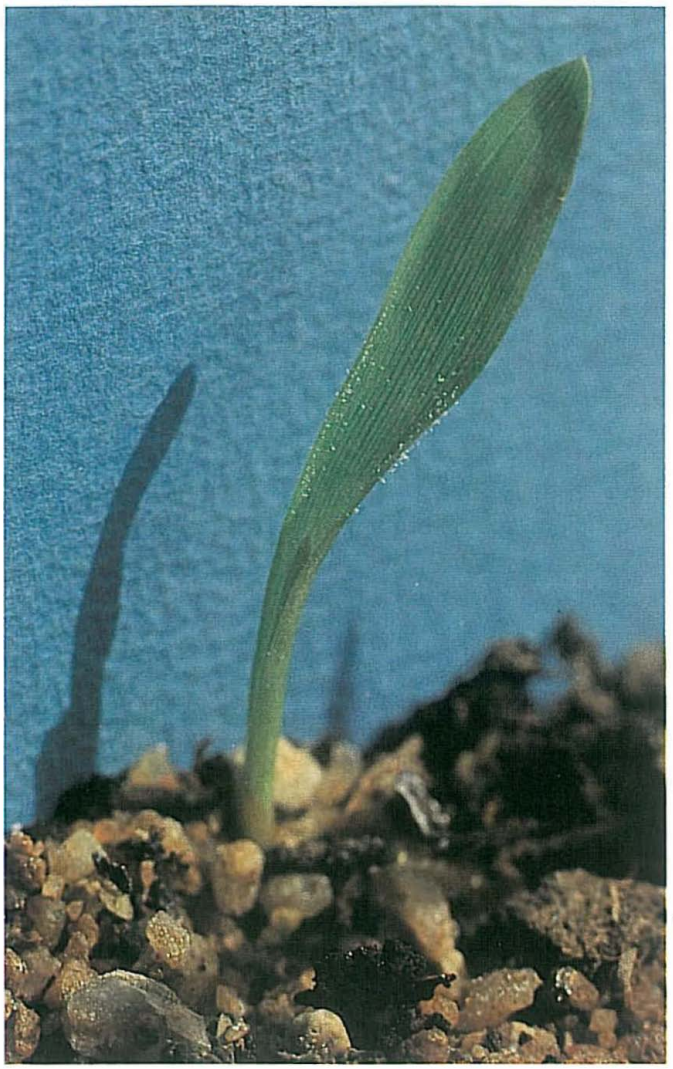

Figure 3. First partially unfolded pearl millet leaf showing asexual growth of *Sclerospora graminicola*.

conditions of severe disease development (Fig. 3). Leaf symptoms begin as chlorosis (yellowing) at the base of the leaf lamina, and successively higher leaves show a progression of greater leaf coverage by symptoms (Fig. 4). The 'half-leaf' symptom (Fig. 5), characterized by a distinct margin between the diseased (basal portion) and nondiseased areas towards the tip, occurs in pearl millet genotypes. It is similar to the half-leaf symptoms caused by *Peronosclerospora sorghi* on sorghum and maize. Under conditions of high humidity and moderate temperature, the infected chlorotic leaf areas support a massive amount of asexual sporulation, generally on the abaxial surface of leaves, giving them a downy appearance. Severely infected plants are generally stunted and do not produce panicles (Fig. 6).

The name 'green ear' stems from the appearance of green panicles due to transformation of floral parts into leafy structures, which can be total or partial (Fig. 7). This is sometimes referred to as virescence. These leafy structures can also be chlorotic, and sometimes support sporulation. In certain cases, green ear is the only manifestation of the disease.

There is a report of artificially induced localized 'green ear' symptoms resulting from panicle inoculation under greenhouse conditions (Semisi and Ball 1989).

Symptoms are rarely seen as local lesions or isolated spots on leaf blades (Saccas 1954, Girard 1975). Spots vary in shape and size, and are at first chlorotic and produce sporangia, and later become necrotic.

Causal Organism

Sclerospora graminicola produces two types of spores, asexual spores known as sporangia (Fig. 8) and sexual spores known as oospores (Fig. 9). The whitish downy growth of the pathogen on the leaf surface is the "asexual phase" (Fig. 10). This phase is generally followed by the "sexual phase" in which oospores are produced within leaf tissues. A comparison of the two spore types is given in Table 2.

Asexual Phase

Sporangiophores are short, stout, determinate, and dichotomously branched structures that emerge from systemically infected leaves through stomata (Fig. 11). Sporangia are produced on sterigmata located at the tips of sporangiophore branches. Fully developed sporangia are hyaline, thin-walled, ellipsoid or broadly elliptic and papillate, with dimensions of 15–22 × 12–21 µm (Saccas 1954, Jouan

Figure 4. A pearl millet plant showing progression of downy mildew symptoms.

Table 2. Differences between oospores and sporangia of *Sclerospora graminicola* on pearl millet.

Oospores	Sporangia
Sexual spores.	Asexual spores.
Produced internally in infected tissue only once.	Produced externally and generally on the lower surfaces of the infected leaves, also produced repeatedly on the same leaf for many days if congenial environment exists.
Survive in soil for several years.	Fragile, die immediately on desiccation, can survive in cold water for several hours.
Primary inoculum, cause primary infection.	Secondary inoculum, cause secondary infection, can also cause primary infection.
Germination by germtube.	Germination by liberation of zoospores.

Figure 5. A leaf showing a typical 'half-leaf' symptom.

and Delassus 1971). However, temperature can affect sporangial size (Singh et al. 1987).

In nature, sporangia are produced in abundance usually during night, between 0100–0400 under moderate temperature and high-humidity conditions. Several workers reported that temperature in the range of 10–25°C was favorable for sporulation (Nene and Singh 1976). It was recently determined that sporangial production can occur between 10 and 30°C with an optimum production at 20°C (Singh et al. 1987). Further, optimum sporangial production occurs between 95 and 100% relative humidity (RH). No sporulation occurs below 70% RH. However, because the environmental conditions for pearl millet cultivation are often hot and dry, even the night environments may not always be conducive to sporangial production. Under optimum conditions of temperature and RH, approximately 1.5×10^5 sporangia can be produced per cm^2 leaf area during one night. Light does not seem to affect sporangial production (Singh et al. 1987).

Sporangia germinate indirectly by producing zoospores. The number of zoospores per sporangium may vary from 1 to 12 (Shetty 1987, Ramakrishnan 1963). Zoospores emerge through a pore produced by the release of an operculum in the apical region of the sporangium. Zoospores swim for 30–60 min, encyst, and then germinate by forming a germtube. Sometimes, zoospores may germinate within the sporangium, in which case the germtube grows through the apical pore giving the appearance of direct germination (Shaw 1981). Sporangia liberate zoospores at a wide temperature range (10–45°C). However, the liberation is optimum at 30°C in about 2 h 40 min. Similarly, germtubes grow at temperatures ranging from 15 to 35°C. Zoospores retain their infectivity for about 4 h at 30°C, and for a

Figure 6. Pearl millet plants severely infected by downy mildew, showing stunting symptoms. Note the production of asexual growth on one of the stunted plants.

Figure 7. Disease-free and malformed earheads (green ears). Note the different types of malformation that can occur.

longer period at lower temperatures (Singh and Gopinath 1990).

Sporangia are ephemeral in nature, and do not survive in the field during daytime. At 5–15 °C, they can survive for about 24 h. However, sporangia are reported to remain viable for about 120 h if suspended in 10% dimethyl sulphoxide and stored at 6 °C (Nene and Singh 1976).

Sexual Phase

The process of sexual reproduction in *S. graminicola* is initiated in antheridia (male) and oogonia (female), and culminates in the formation of oospores. Oospores are produced in large numbers. The oosporic wall has three distinct layers: the exosporium, the mesosporium, and the endosporium. As a rule, in *Sclerospora* spp. the oogonial wall is fused with the oospore wall, which is a major identifying feature of this genus. The mature oospore is spherical and brownish yellow, and measures 32 µm (22–35 µm) in diameter (Fig. 12, Fig. 9).

Two mating types have been identified and are considered to be necessary for the production of oospores, illustrating the heterothallic nature of the pathogen (Michelmore et al. 1982). Further, mating types produced by collections of the pathogen from South Asia are compatible with those produced by collections of the pathogen from western Africa (Idris and Ball 1984). However, there is also some evidence of the existence of homothallism in *S. graminicola* (Michelmore et al. 1982).

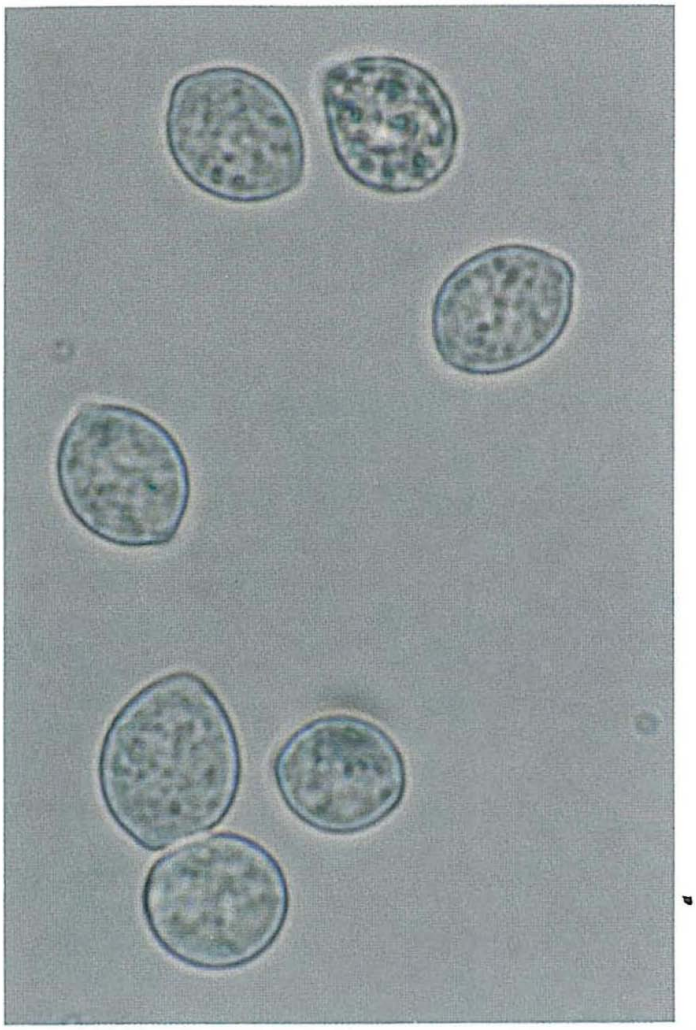

Figure 8. Typical asexual spores (sporangia) of the downy mildew pathogen (× 132).

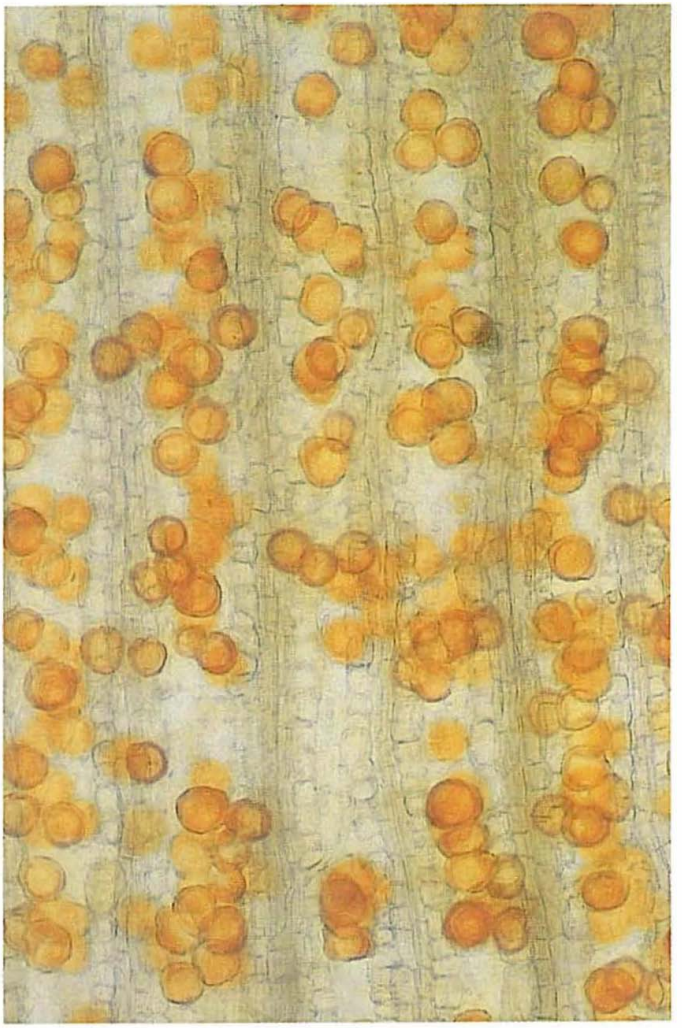

Figure 9. An infected leaf containing sexual spores (oospores) of the downy mildew pathogen (× 33).

Oospores are resting spores. The thick oospore wall protects them from desiccation, and probably serves as an impermeable membrane. Reports suggest that oospores can survive from 8 months to 10 years under laboratory conditions (Nene and Singh 1976). The wide differences in reports on the length of survival may be the result of production on different varieties, under different environmental conditions, extent of attack by mycoparasites, or the interaction of several factors.

Many workers have reported on the germination of oospores, both directly by germtubes and indirectly by the liberation of zoospores, with great variation in the frequency of germination (Nene and Singh 1976). However, these results have generally not

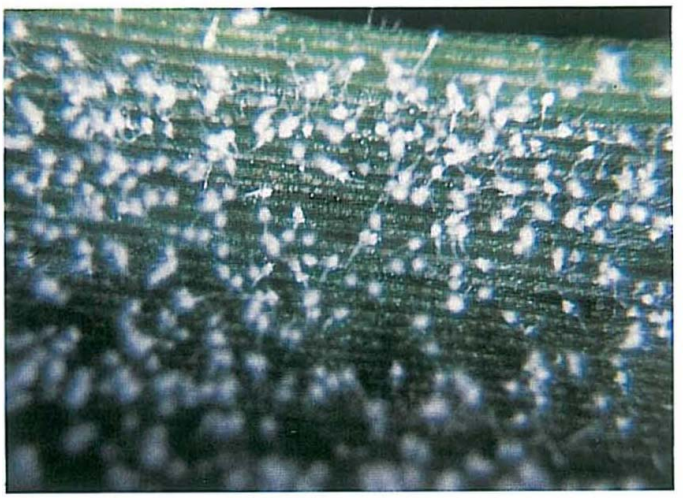

Figure 10. An abaxial surface of pearl millet leaf showing asexual growth (sporangia and sporangiophores) of downy mildew fungus (× 16.5).

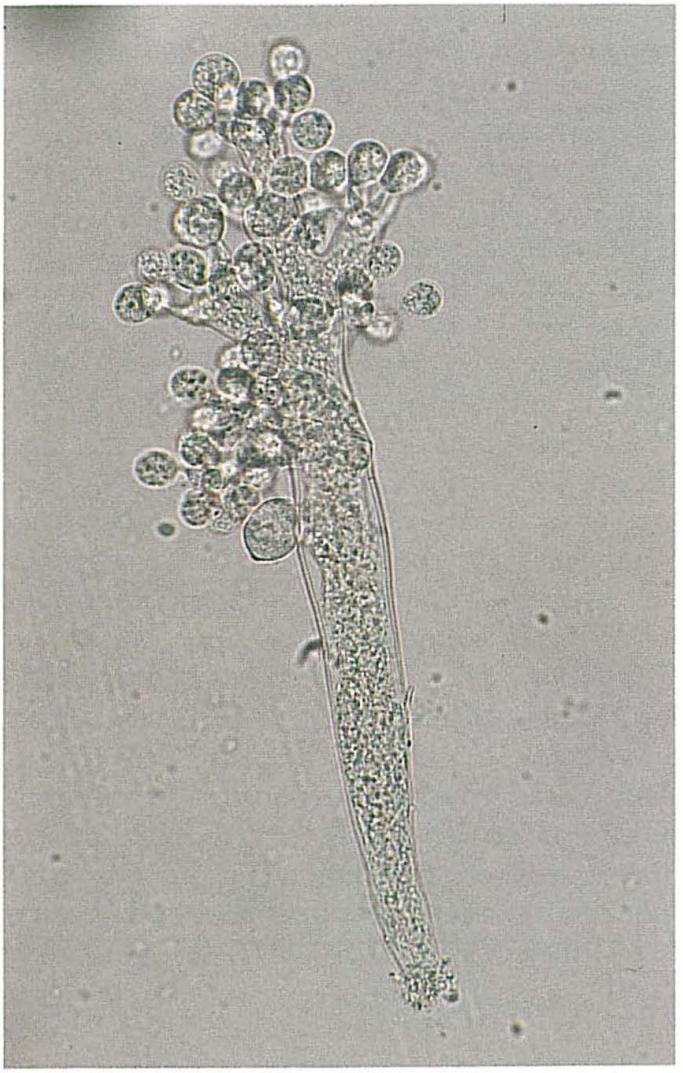

Figure 11. A fully developed sporangiophore bearing sporangia (× 66).

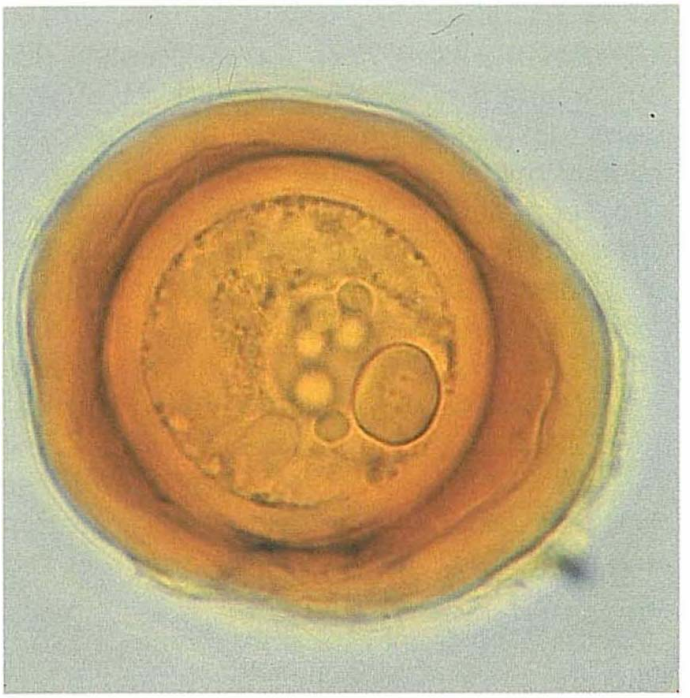

Figure 12. A fully developed oospore of the downy mildew pathogen (× 330).

been reproducible. Recently, however, Panchbhai et al. (1991) reported obtaining up to 76% germination when oospores were treated with sodium hypochlorite (Clorox®) (Fig. 13).

Pathogenic Variability

Like other obligate parasites, *S. graminicola* has an inherent mechanism to develop variability. The pathogen survives through sexually produced oospores which are genetic recombinants. Further, the pathogen is heterothallic with two mating types. The pathogen populations can therefore be highly variable and adaptable.

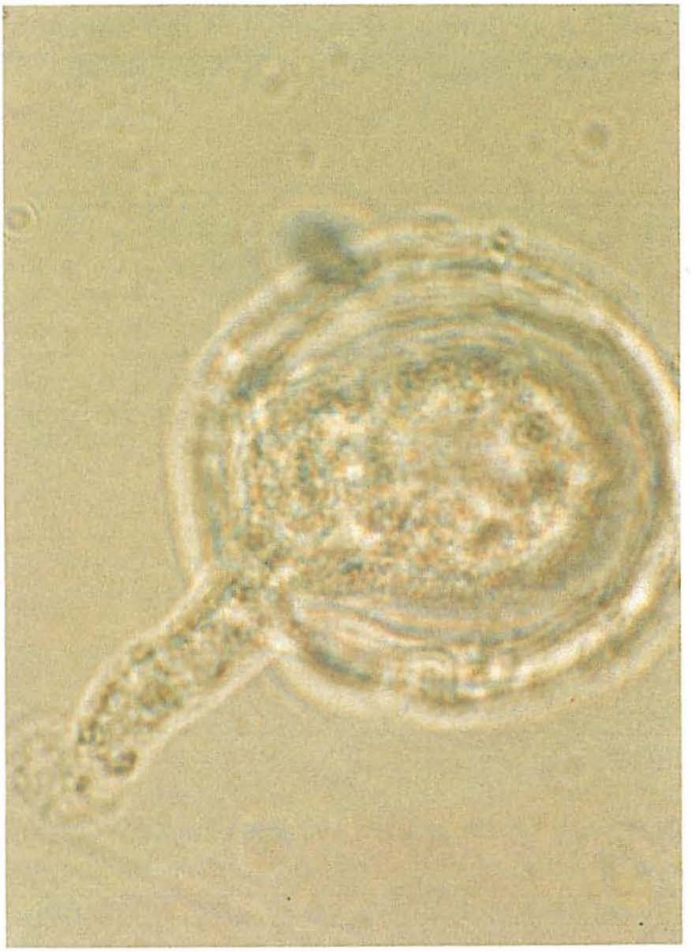

Figure 13. A germinating oospore (× 330).

The first report of pathogenic variability in *S. graminicola* came from Karnataka state (India), where NHB 3, a popular hybrid, was found to be susceptible to the Gulbarga population of the pathogen, but resistant to the Mysore population (Bhat 1973). Pathogenic variability was reported later by Girard (1975) in western Africa and Shetty and Ahmad (1981) in India. Locational differences in virulence have also been found in the International Pearl Millet Downy Mildew Nursery (IPMDMN), the West African Downy Mildew Variability Nursery (WADMVN), and the West African Downy Mildew Observation Nursery (WADMON), which are operated annually.

In IPMDMNs, many entries developed consistently more disease in Nigeria and Niger than in other countries of western Africa or in India. The WADMVN conducted during four seasons at seven locations in western Africa showed locational and varietal differences with the highest disease pressure in Cinzana (Mali) and Bengou (Niger), and the lowest in Bambey (Senegal) (Table 3). It has been shown by Werder and Ball (1992) and King et al. (1989) that some genotypes such as MBH 110, NHB 3, and 81 B (ICMB 1) differ in their downy mildew reactions between locations and pathogen populations. This is further evidence of the differences in the virulence of *S. graminicola* in western Africa and India. Virulence differences were also found in greenhouse tests in the United Kingdom, in which oospore collections from Africa and India were compared under the same environment, (Ball 1983, Ball and Pike 1983). Singh and Singh (1987) provided evidence that *S. graminicola* is highly cultivar-specific. They conducted a study with NHB 3, which was grown quite extensively in the state of Rajasthan. NHB 3 was last grown in 1977 in a sick plot at Durgapura, and was again grown after a gap of 3 years, in 1980. Up to 1977, it was highly susceptible, but in 1980 it remained free of disease. Based on several experiments conducted under controlled conditions, they concluded that a pathogen population specific to a particular cultivar can disappear within 3 years if the cultivar is withdrawn from cultivation

Table 3. Mean downy mildew incidence (%) of 11 pearl millet genotypes tested at seven locations in western Africa (WADMVN), rainy seasons 1986–1989.

	Downy mildew incidence (%) at dough stage[1]							
Entry	Bambey	Bawku-Manga	Bengou	Cinzana	Ina	Kamboinsé	Samaru	Mean
ITMV 8001	0	1	14	16	2	8	7	7
ITMV 8304	1	4	14	12	5	6	11	7
700651	0	1	8	32	7	10	4	9
IKM/CVP 39/83/84/351	0	5	2	40	7	1	8	9
INMV 8220	2	10	13	31	3	1	5	9
IKMV 8201	3	11	10	29	15	7	3	11
WC-C75	1	31	20	35	15	11	11	18
81B	34	1	90	42	49	4	53	39
ICMS 8410	2	-[2]	81	47	64	2	37	39
MHB 110	5	66	52	48	46	54	17	41
NHB 3	2	73	25	61	29	50	54	42
Mean	4	20	30	36	22	14	19	

1. Downy mildew incidence represents mean of four seasons (1986–1989), except Bawku-Manga (1987, 1988) and Ina (1988).
2. - = Not tested.

Table 4. Downy mildew incidence (%) in 7042 and NHB 3, inoculated with oospores and sporangia of the downy mildew pathogen from Durgapura and ICRISAT Center.

		Oospore inoculum			Sporangial inoculum		
Cultivar	Oospore inoculum source	No. of plants	Downy mildew (%) at 28 DAI[1]	SE	No. of plants	Downy mildew (%) 14 DAI[1]	SE
7042	Durgapura	119	54[2]	±4.6	67	71[3]	±5.6
NHB 3	Durgapura	122	0[2]		68	14[3]	±4.2
7042	ICRISAT Center	86	54	±5.9	60	92	±3.9
NHB 3	ICRISAT Center	134	68	±4.0	60	98	±1.8
Noninoculated controls							
7042		107	0		45	0	
NHB 3		19	0		44	0	

1. Days after inoculation.
2. Means of two tests.
3. Means of three tests.

(Table 4). Similar results were obtained when NHB 3 was grown after a gap of several years in Nakshatrawadi area in Maharashtra (Table 5). This information, if confirmed at other locations, and if confirmed with other hybrids, could provide a basis for the recycling of pearl millet cultivars for the management of the downy mildew disease (S.D. Singh, unpublished).

Table 5. Downy mildew incidence[1] (%) of two susceptible controls, NHB 3 and 7042, at Patancheru, Mysore, and Aurangabad and of MBH 110 only at Aurangabad, during the 1988 rainy season.

Entry	Patancheru	Mysore	Aurangabad[2]
NHB 3[3]	95	97	0
7042[4]	94	66	61
MBH 110	-[5]	-	52

1. Mean of five replications.
2. Results are from a farmer's field where MBH 110 showed a high degree of susceptibility in 1987.
3. NHB 3 and HB 3 are genetically similar.
4. Universally susceptible control.
5. - = Not evaluated.

Disease Cycle

Oospores, which are the source of primary inoculum, remain in the soil and infect the underground parts of plants, mostly at the seedling stage. The exact site of entry of oospore inoculum is not known, but it is believed that after penetration, the pathogen soon colonizes the growing point. Subsequent to invasion of the growing point, systemic symptoms appear in leaves and panicles produced by the growing point. Although the appearance of disease symptoms may depend to a large degree on the environment, under field conditions, systemic infection has been observed within 6

days after sowing. Infected plants produce oospores which are transmitted on the seed surface, in soil, by wind, or by water.

Under humid conditions, systemically infected leaves produce abundant sporangia on the abaxial surface. Sporangia are important for the secondary spread of the disease within and among fields if environmental conditions are suitable (Singh and Williams 1980). These sporangia germinate and produce zoospores, which in turn, germinate and cause infection. Germtubes generally penetrate the epidermis between cells but they can enter through the stomata also (Bhatnagar, 1988). Sporangial infectivity is limited by seedling age, with the greatest susceptiblity from the time of seed germination to the 1–2 leaf stage. Thereafter, the susceptibility decreases sharply (Singh and Gopinath 1985). Inoculation of plants at the coleoptile stage produces systemic symptoms in young leaves 4–7 days later. If the environment is suitable, infected leaves continue to produce sporangia until the tissues become necrotic or senesce. Oospores are produced in infected leaves when compatible mating types of *S. graminicola* are present in the same tissue, or when homothallism is operative. Oospores are not always found in systemically infected leaf tissue, presumably because only one mating type is present and homothallism is inoperative. Oospores remain in the soil along with infected leaf residue, and

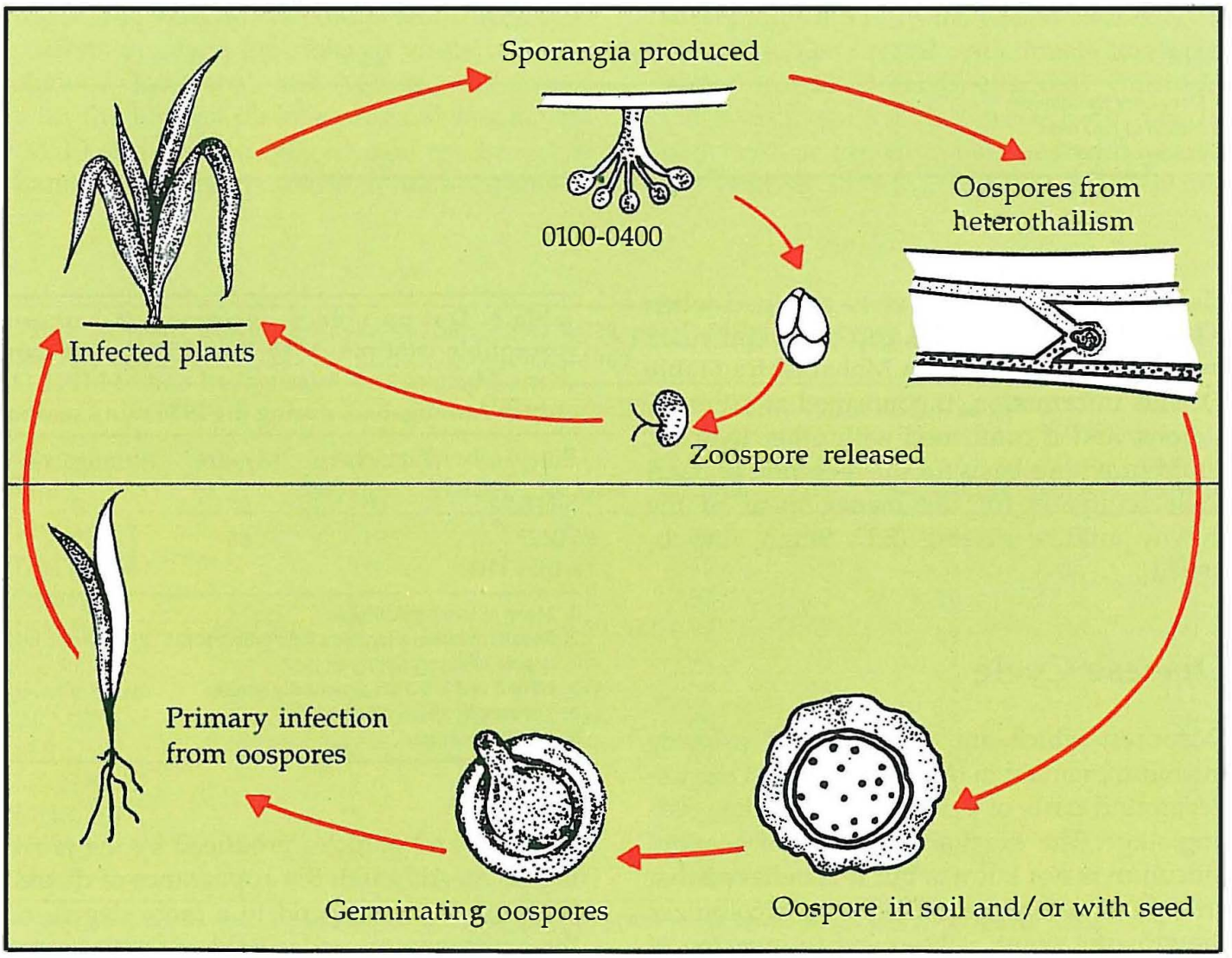

Figure 14. Annual recurrence of downy mildew under field conditions.

cause primary infection in the following years (Fig. 14).

Host Range

Although 14 graminaceous species belonging to eight genera have been reported as hosts of *S. graminicola* (Bhat 1973) (Table 6), their importance in the disease epidemiology is not clear. Shetty (1987) and Suryanarayana (1965) reported the production of sporangia and oospores on *Setaria verticillata* in India. Singh and Williams (1979a) tested 23 entries belonging to 11 genera including *Sorghum vulgare, Pennisetum americanum* (Syn = *P. glaucum*), *Zea mays, Paspalum* sp., *Setaria italica, Eleusine coracana, Heteropogon contortus, Echinochloa* sp., *Panicum miliaceum, Panicum miliare,* and *Euchlaena maxicana.* However, none of these except *P. glaucum* developed downy mildew under downy mildew nursery conditions at ICRISAT Center, in which a downy mildew-susceptible control, 7042, developed 100% downy mildew. Cultivars of all these genera, except *Echinochloa* sp., were also tested using a seedling dip inoculation technique (S.D. Singh, unpublished), but none developed downy mildew except the cultivars belonging to *Pennisetum glaucum.* Oospores of *S. graminicola* from *S. italica* failed to infect 7042. These examples clearly show a degree of host-specificity in *S. graminicola* of pearl millet (Singh and Luther 1981). This suggests that the reported hosts do not play a role in the disease epidemiology.

In the United States, *S. graminicola* has been reported in the field on *Setaria* spp. and in the greenhouse on maize, but it has not been reported on pearl millet (Melhus et al. 1928).

Table 6. Host range of *Sclerospora graminicola.*

Host	Tribe
Zea mays Linn.	Maydeae
Saccharum officinarum Linn.	Andropogoneae
Echinochloa crusgalli var. *frumentacea* (Roxb.) W.F. Wight	Paniceae
Panicum miliaceum Linn.	Paniceae
Pennisetum leonis Stapf & Hubb.	Paniceae
Pennisetum spicatum (Linn.) Roem. & Schult.	Paniceae
Pennisetum typhoides (Burm.) Stapf & C.E. Hubb.	Paniceae
Setaria italica (Linn.) P. Beauv.	Paniceae
S. lutescens (Weig.) F.T. Hubbard	Paniceae
S. verticillata (Linn.) P. Beauv.	Paniceae
S. viridis (Linn.) P. Beauv.	Paniceae
Euchlaena maxicana Schrad.	Maydeae
S. magna Griseb [*Chaetochloa magna* (Griseb) Schribner]	Paniceae
Agrotis alba auctt. non Linn.	Agrostideae

Source: Bhat 1973.

Seed Transmission

Transmission of downy mildew by seed has been a subject of controversy. Although it is believed that the disease is seed-borne in the form of seed-carried oospores, internal seed transmission of the disease has not been accepted by all. There are reports for and against it (Suryanarayana 1962, Arya and Sharma 1962, Sundaram et al. 1973, Safeeulla 1976, Thakur and Kanwar 1978, Shetty et al. 1980). Although mycelium has been found inside the seed (Singh 1974, Safeeulla 1976), grow-on tests have shown that this mycelium does not result in systemically infected seedlings (Williams 1984).

Epidemiologically, the reported level of internal seed transmission may or may not be significant. What is more important, however, is the presence of qualitatively different populations between India and Africa, among African countries, and the absence of this pathogen on pearl millet in the Americas. This necessitates precaution in the movement of seed from one country to another. Indian Plant Quarantine authorities and ICRISAT have developed, and are using the following seed treatment procedures to eliminate any possi-

ble introduction of *S. graminicola* through seed from other countries.

1. Seed is treated for 10 min with 0.1% $HgCl_2$ with several rinses in distilled sterile water.
2. Seed is then given a hot water treatment at 55°C for 12 min followed by drying under shade.
3. Seed is then treated with metalaxyl at 2 g a.i. kg^{-1} seed.

After the above treatment, seed is sown in the post-entry quarantine isolation area (PEQIA) at ICRISAT Center, and observed for downy mildew occurrence from emergence until maturity. So far, no downy mildew occurrence has been observed on any imported accession since 1977.

Mycoparasites

Several mycoparasites on the downy mildew pathogen have been reported. Raghavendra Rao and Pavgi (1976) reported *Fusarium semitectum* on green ears. This mycoparasite produces pinkish-white, diffuse spots which enlarge into patches of pinkish, powdery growth, often covering the entire surface of the green ears, particularly under humid conditions. Most of the oospores from the affected green ears are invaded by the mycoparasite, reportedly at all developmental stages. The infected oospores were killed, their walls collapsed, and their identity changed. Proliferated structures did not produce asexual growth. In another case, Balasubramanian (1980) reported that *Drechslera setariae* parasitized pearl millet leaves systemically infected with downy mildew. This parasitic relationship was first observed as small flecks (1 mm diameter) which increased in size (3–10 mm × 1–5 mm) over time. The lesions coalesced, eventually covering the entire infected area. Young seedlings were killed, giving a false impression of death due to downy mildew. Downy mildew-free leaves were not infected by *D. setariae.* Recently, lesions caused by *Fusarium longipes* were also found in the leaf tissue of pearl millet systemically infected with downy mildew (S.S. Navi and S.D. Singh, personal communication). This mycoparasite grows very quickly under high humidity and an overcast sky, or under continual rains, covering the entire infected area. Young seedlings are killed prematurely. Asexual sporulation is stopped almost completely and oospores are parasitized (Fig. 15).

Figure 15. Oospores parasitized by *Fusarium longipes*, a mycoparasite on the downy mildew pathogen. The contents of the oospores are completely destroyed by the pathogen (× 132).

Another Downy Mildew Pathogen on Pearl Millet

Kenneth and Kranz (1973) reported that *Plasmopora penniseti* also caused downy mildew on pearl millet. This downy mildew was first observed at the Boko Experiment Station in Ethiopia. The first symptoms are small, diffused, water-soaked stripes or spots (0.5–1 mm) which expand to irregular, interveinal stripes (1–2 mm × 60 mm or more). Stripes can coalesce and render parts of the lamina necrotic, and finally the stripes may enlarge beyond the veins into large spots which turn grayish brown. There was profuse asexual sporulation, but no oospores were observed.

The disease was found in a remote area of the Ethiopian highlands (around 1600 m) where pearl millet was introduced in 1966. It was reported that the seed had been imported from India. However, the pathogen has not so far been reported in India or elsewhere.

Control Methods

Control measures have been designed to reduce the movement of primary soil and seed-bearing oosporic inoculum and the secondary spread of sporangia within and between pearl millet fields. The methods used to control downy mildew can be classified into three categories: cultural, chemical, and host-plant resistance.

Cultural

All cultural control methods are aimed at manipulating the environment to the advantage of the host and disadvantage of the pathogen. Five such methods have been suggested to control pearl millet downy mildew.

Sanitation

Use of disease-free seed and effective reduction of oospore-infested debris after harvest of the crop are essential to reduce primary inoculum in the soil in the succeeding years. There is a possibility of seed being contaminated with oospores which adhere to the seed surface during harvesting and threshing. This contamination can be inactivated by treating contaminated seed with metalaxyl before sowing. A procedure to inactivate seed-borne inoculum, both internal and external, has been developed and detailed earlier in this bulletin. This procedure, however, is impractical with large seed quantities.

Downy mildew-infected plant debris should be burnt, or the field should be plowed deeply to bury the debris. This will help reduce oospore concentration in the upper root zone where infection is most likely to occur. Deep plowing is not generally followed by farmers, because it is difficult or because of the expense involved.

Early Sowing

A pearl millet crop sown very early in the season generally has less downy mildew than that sown late in the season (Chahal et al. 1978b). In pearl millet-growing areas, sowing is usually done with the first sufficient rains. During this time, temperatures are generally higher, and rainfall and RH lower than later in the rainy season when rains become more frequent. It is not known whether oospore germination is reduced during these conditions of infrequent rains and higher temperatures. However, it is known that hot and dry conditions reduce secondary spread by reducing sporangial production and their infectivity. Though early sowing is likely to favor disease escape, time of sowing is not practical and cannot be easily manipulated by the pearl millet farmer.

Direct Sowing vs Transplanting

A transplanted crop of pearl millet suffers significantly less from downy mildew than a di-

rect-sown crop, both in the rainy and post-rainy seasons (Chandrasekhara Rao et al. 1987). This method can therefore be used to reduce downy mildew where transplanting of pearl millet is practised.

Roguing

Removal and destruction of infected plants when they appear has been recommended for the control of downy mildew (Thakur 1980). This method can reduce the production of sporangia, and therefore, reduce the spread of the disease during the same season (Singh and Williams 1980). It also reduces oospore buildup for the following season. Since there are no known collateral hosts, destroying infected pearl millet plants as they appear could reduce the buildup of epidemics, but farmers should be able to detect infected plants at an early stage and they would have to be convinced that the return in increased downy mildew control would be worth the extra effort.

Nutrition

There have been studies on the effects of N, P, and K fertilizers on downy mildew when applied singly and in various combinations, to soil and to foliage as sprays. However, the results obtained have been inconsistent (Deshmukh et al. 1978, Singh 1974, and Singh and Agarwal 1979). In any case, it is doubtful whether resource-poor pearl millet farmers will ever be able to use N,P, and K fertilizers for the control of downy mildew in pearl millet.

Chemical

Considerable research has been done to control downy mildew by both protective and systemic fungicide applications. These fungicides were applied to the soil to control soilborne infection, to the seed to control seedborne infection, and to the above-ground plant parts to control airborne infection.

Although protective fungicides (such as Zineb® and Maneb® applied to seed and leaves) may reduce the disease to some extent (Suryanarayana 1965, AICMIP 1967–1972), there is no economic return on this approach to control downy mildew (Ramakrishnan 1963, and Singh 1974). The reason for this failure could be the inability of these fungicides to withstand frequent rains when applied as sprays, and their failure to protect shoots and roots from systemic infection after their application to seed (due to lack of systemic action).

The systemic fungicide metalaxyl [methyl DL- (2, 6-demethyl phenyl)-N (2, methoxyacetyl)-N-alaninate] has been used successfully to control downy mildew in pearl millet. Seed treatment with metalaxyl at 2 g a.i. kg^{-1} seed controlled the disease excellently (Fig. 16) for about the first 35 days after sowing (Venugopal and Safeeulla 1978, Muthuswamy and Narayanaswamy 1980, Williams and Singh 1981, Singh 1983b, Dang et al. 1983). As a seed treatment, metalaxyl controls soil- and seedborne inoculum, and is absorbed by the seedlings, protecting them from early sporangial infection. Foliar application of the fungicide at 125 mg L^{-1} a.i. arrests further development of the disease in systemically infected plants, and if applied before floral initiation, disease-free heads (recovery from systemic infection) are produced (Singh and Williams 1979b, Singh et al. 1984). Plants grown in a greenhouse can be recovered by spraying 31 mg L^{-1} a.i. of metalaxyl, but a higher concentration is needed to recover field-grown plants because of continuous inoculum availability under field conditions. Recovery resulting from foliar spray with metalaxyl can be achieved at any age, but panicle length can be reduced if the diseased plants are sprayed during or after panicle development (Singh et al. 1984). Recent studies showed that seed treatment with metalaxyl, coupled with a single foliar application of metalaxyl + mancozeb® was much superior to the seed treatment alone (Shankara Rao et al.

Figure 16. Two NHB 3 plots grown with and without seed treatment with metalaxyl. The untreated NHB 3 hardly produced any heads under severe disease pressure.

1987). Metalaxyl seed treatment and foliar spray may not be practical for farmers for the control of downy mildew in a crop grown for grain. However, it is highly economical for commercial seed production fields and for experimental purposes, such as the production of seed of highly susceptible materials for inheritance studies or germplasm maintenance.

Host-plant Resistance

Use of resistant cultivars is the most cost-effective method for the control of downy mildew. Considerable progress has been made in the development of screening techniques, identification of sources of resistance, and breeding of resistant cultivars.

Screening Techniques

Screening techniques which are reliable in the identification of resistance, and well adapted to breeding procedures are essential for a successful pearl millet improvement program.

Field screening. A field-screening technique which mainly utilizes sporangia as infection propagules was developed (Williams et al. 1981). It is desirable to use the same field each year to encourage a buildup of oospore inoculum in the soil (as in a sick plot). This technique has three basic components:

1. **Infector rows** (inoculum donors), which are mixtures of two to three susceptible genotypes (local landraces and universally susceptible material), are sown before the

test material. In some places including at ICRISAT Center, infector rows are sown on every ninth row through the entire length of the field, and in others, they are sown at every fifth row. At ICRISAT Center, we now routinely spray-inoculate infector rows at the coleoptile- to one-leaf stage with a sporangial suspension (10^5 sporangia mL^{-1}) during late evening hours after irrigation, to encourage a higher frequency of infected plants at an early growth stage.

2. **Test rows** are the material to be tested. These are sown in the intervening rows after the infector rows have developed 50–60% disease. Test rows are usually sown 3–5 weeks after infector rows are sown.

3. **Indicator rows** (susceptible genotype), which indicate the level of disease pressure in the nursery, are sown along with the test material at regular intervals (generally every 10–30 rows).

It is necessary to provide some form of irrigation (perfospray, sprinkler, furrow) to build up high relative humidity for sporangial production, and for the infection processes to occur. The field-screening technique provides uniform distribution of sporangial inoculum throughout the test material during the period of greatest vulnerability (early seedling stage) in a natural manner.

This field-screening technique is being used twice a year (rainy and postrainy seasons) at

Figure 17. An aerial view of a downy mildew field-screening nursery at ICRISAT Center. The taller rows running across the field are infector rows. The younger crop sown in between the infector rows are the test material. Note the presence of susceptible indicator rows amongst the test material. In the background is the pearl millet breeding nursery.

ICRISAT Center. In Niger, it is being used each year at Bengou (June to September) and at ISC (Sadoré) from August to November. It is now also being used in national programs in India and western Africa (Fig. 17).

Greenhouse and laboratory screening. Various greenhouse and laboratory screening techniques have been developed, generally involving plants at the seedling stage. These are useful where more precise studies are required (controlled RH and temperature, and inoculum concentration and placement), or for mass screening of breeding materials. Singh and Gopinath (1985) developed a technique which involves inoculation of potted seedlings in the coleoptile stage (<10 mm above ground) using a microsyringe (Fig. 18). A drop of inoculum (10^5 sporangia mL^{-1}) is placed at the apex of the coleoptile and allowed to flow down to the base covering most of the above-ground surface area of each plant. Inoculated seedlings are then kept at about 20°C and >95% RH for 12–16 h, after which they are transferred to a greenhouse. The inoculated seedlings are identified (using toothpicks or match sticks) to differentiate them from those that may emerge later. Under favorable conditions, >90% of the susceptibility of a genotype is expressed within 15 days after inoculation.

Another seedling-screening technique, specifically designed for mass screening of breeding materials, involves spray-inoculation of potted plants at the coleoptile to one leaf-stage with a sporangial suspension (about 10^5 sporangia mL^{-1}) (Fig. 19). The pots are incubated overnight at about 20°C and >95% relative humidity, by covering the pots with plastic sheet. The pots are then kept on greenhouse benches. Seedlings are evaluated for downy mildew incidence about 2 weeks after inoculation, when infected plants show mottling and chlorosis in leaves. Sporangial production may not be evident unless the RH during night exceeds 90%. This technique permits screening of large numbers of plants relatively easily and at a convenient time, such as during the offseason and before breeders sow their next crop. It is being used extensively to screen breeding material at ICRISAT Center and for preliminary screening tests at ISC.

Figure 18. A seedling inoculation technique: a precise method of inoculation of seedlings with sporangia. Each seedling is inoculated with a known volume of inoculum.

Identification of Resistance

At ICRISAT Center, 3163 accessions from the Genetic Resources Unit originating from more than 25 countries in the major millet-growing areas of the world, have been screened. A total of 428 accessions with high levels of resistance and which flower in 45–60 days at ICRISAT Center, were further evaluated, and 48 single-plant selections made. Progenies of these

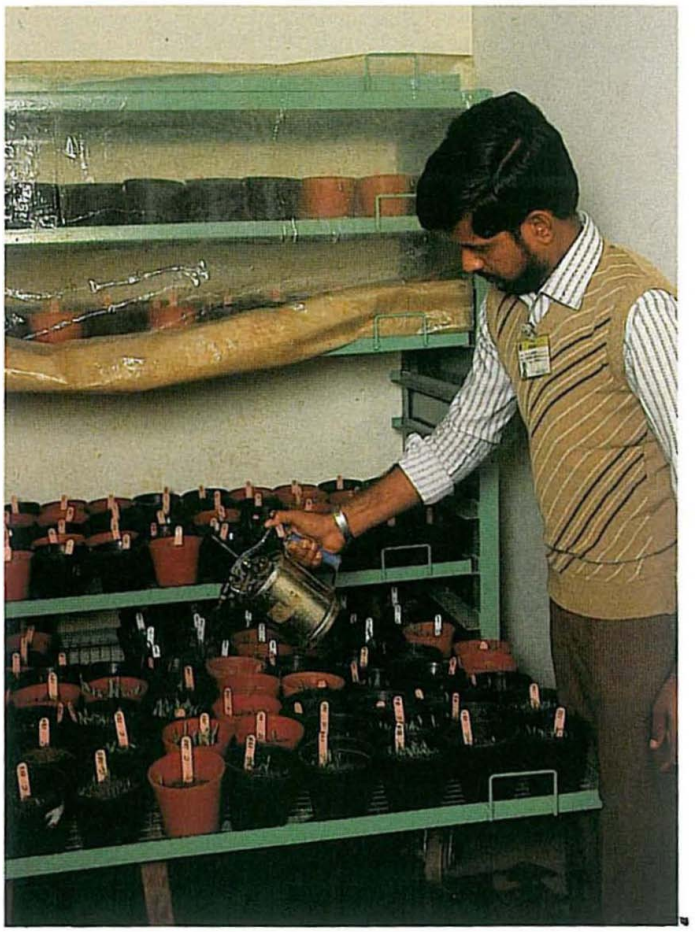

Figure 19. A method of mass inoculation of seedlings with sporangia. This method is now being used routinely to screen large numbers of breeding materials under greenhouse conditions.

selections were highly resistant and agronomically acceptable, and are available as a major source of downy mildew resistance for future breeding in India (Singh 1990). In addition, many sources of resistance have been identified in India by other workers (Appadurai et al. 1978, Chahal et al. 1975, Chahal et al. 1978a, Dass and Kanwar 1977, Deshmukh et al. 1978, Shinde and Utikar 1978). At ISC, no attempt was made to identify specific sources of resistance.

Sources of Stable Resistance

A number of sources of stable downy mildew resistance have been identified with the help of cooperators in India and western Africa. The IPMDMN has been in operation since 1976 at downy mildew hot-spot locations in India and Africa, involving 25–45 entries from breeders and pathologists each year. More than 50 sources of stable resistance, primarily originating from Nigeria, have been identified, and seven of these (Table 7) possess an extremely high degree of stable field resistance (Singh et al. 1990).

The West African Downy Mildew Disease Nursery (WADMDN) has been conducted in collaboration with national programs in western Africa since 1986. Each year national programs and ISC contribute promising entries to be tested for stable resistance in western Africa. Some of the tested entries, such as SE 2124, SE 13, and T 18L, have shown stable resistance (Table 8).

We recently identified seven pearl millet accessions (IP 18292 to IP 18298) that showed 100% resistance to three major pathotypes of India (Mysore, ICRISAT Center, and Aurangabad). During initial tests in Niger and Mali in western Africa, five of these accessions remained free from the disease in pots and in downy mildew nurseries for about 30 days after sowing. All these genotypes possess some morphological trait that will help maintain the purity of the line (Fig. 20a and b).

Use of Resistance

At ICRISAT Center, resistant sources are being used, particularly in the hybrid program. SDN 503 [ICML 13], P 7 [ICML 12], 700516 [ICML 15], P 310, and 700651 (ICML 16) are being used in breeding pollinators, while resistance from P 7 and 700651 is being transferred into hybrid seed parents. ICML 16 is a constituent of two varieties, ICMV 2 and ICMV 3, which were released in Senegal. Similarly, several resistant sources, including ICML 15 and P 310 have been used in breeding programs in southern Africa.

In population breeding at ICRISAT Center, progenies of composites are tested and selected in the downy mildew nursery and in greenhouse screening. The levels of downy

Table 7. Reactions of seven sources of stable resistance to downy mildew (*Sclerospora graminicola*) across years and locations.

Accession	ICRISAT PMIC No.	Downy mildew severity (%)[1]												
		1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988
P 7	ICML 12	2	2	2	3	2	1	4	1	-[2]	-	-	-	
SDN 503	ICML 13	1	1	2	3	4	2	7	1	-	-	-	-	-
700251	ICML 14	2	1	1	1	3	2	3	1	-	-	-	-	-
700516	ICML 15	1	1	2	1	1	1	3	1	-	-	-	-	-
700651	ICML 16	1	1	2	1	1	1	3	1	-	-	-	-	-
P 1449	-	-	-	-	-	-	-	-	-	1	3	1	1	3
P 310	-	-	-	-	-	-	-	-	1	1	4	1	1	4
Control[3]		61	58	69	47	61	42	60	50	48	39	44	39	57

1. Values indicate mean downy mildew severities over 6–12 locations per year in India and western Africa (only Indian locations in 1983).
2. - = Not tested.
3. Downy mildew-susceptible control (NHB 3, HB 3, or 7042).

mildew resistance in the composites have increased substantially, so incorporation of resistance from other sources is currently not being pursued. At ISC, progenies of population breeding are tested in the downy mildew nursery at Bengou and Sadoré, Niger. In addition, male-sterile lines are evaluated for downy mildew reaction in order to develop topcross hybrids for western Africa (Anand Kumar and Werder 1989).

Table 8. Reactions to downy mildew, of pearl millet varieties tested multilocationally in western Africa, rainy seasons 1986–1989.

Entry	Institute and country[2]	Downy mildew incidence (%)[1]				
		1986	1987	1988	1989	Mean
SE 2124	IAR, Nigeria	2	3	-[3]	-	2.6
SE 13	IAR, Nigeria	-	4	3	-	3.8
T 18L	INRAN, Niger	3	6	-	8	5.4
SE 361	IAR, Nigeria	-	5	6	-	5.6
GRP 1	INRAN, Niger	-	5	8	7	6.8
SE 75	IAR, Nigeria	8	-	6	-	7.0
SE 360	IAR, Nigeria	3	18	6	-	8.8
Composite precoce	IER, Mali	-	4	14	-	8.9
IKMV 8201	INERA/ICRISAT, Burkina Faso	9	-	10	-	9.3
Control[4]		30	53	77	86	61.5

1. Values indicate mean downy mildew incidence over five to seven locations per year in West Africa.
2. IAR = Institute for Agricultural Research; INRAN = Institut national de recherches agronomiques du Niger; INERA = Institut national d'études et de recherches agricoles; IER = Institut d'économie rurale.
3. - = Not tested.
4. Downy mildew-susceptible control NHB 3 or 7042.

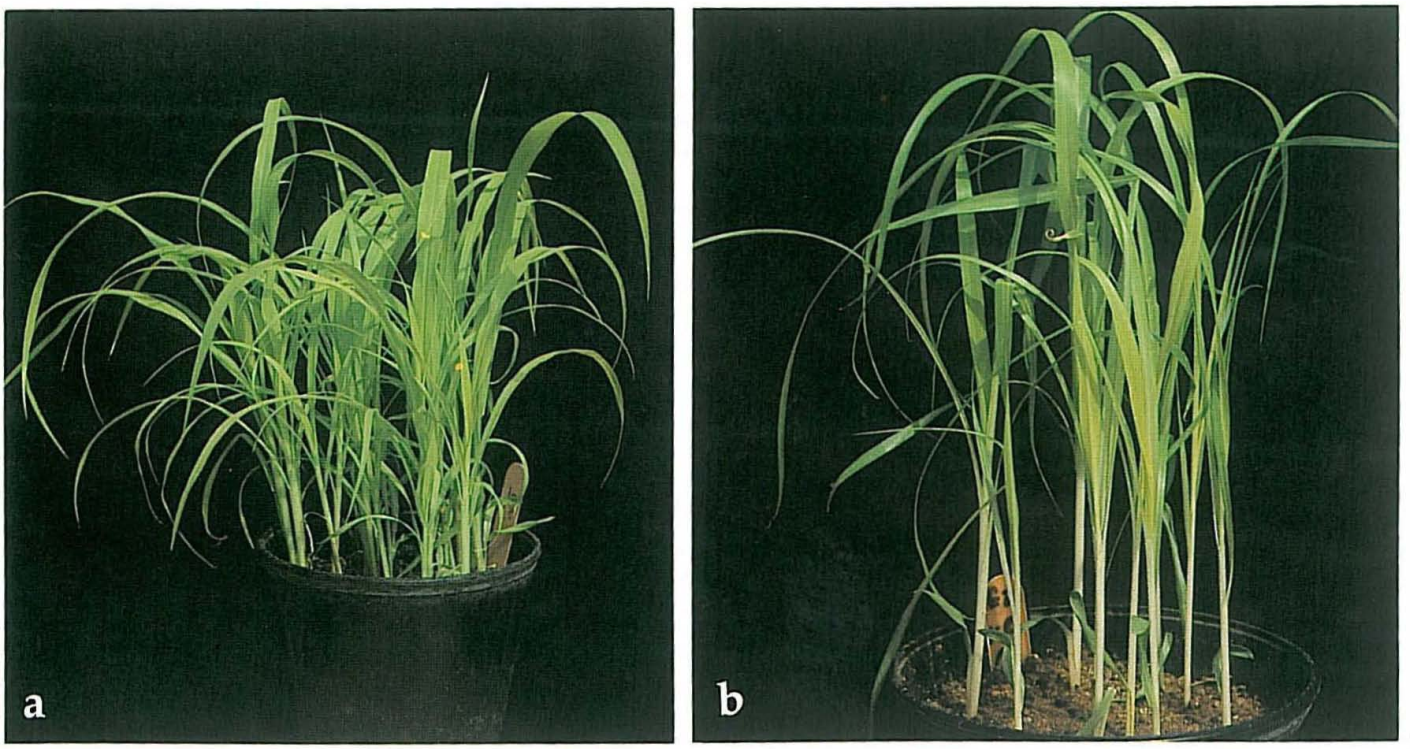

Figure 20. Two of the seven newly identified sources of resistance to downy mildew; (a) yellow seedlings, and (b) seedlings with white leaf sheath.

Resistant Cultivars Produced and Grown by Farmers

Four open-pollinated varieties developed at ICRISAT Center, WC-C75, ICMS 7703, ICTP 8203, and ICMV 155, have been released for cultivation in India. WC-C75 has been cultivated by Indian farmers since 1983, and has been grown annually in nine states on a total of over 1 million ha. There is no authentic report yet, of its resistance becoming ineffective, in contrast to the 'breakdown' of resistance of several hybrids in India during this period. In western Africa, ICRISAT has developed, in collaboration with Institut national d'études et de recherches agricoles (INERA), the national program in Burkina Faso, some promising downy mildew-resistant varieties such as IKMP 3, IKMP 2, and IKMV 8201 for widespread on-farm tests (Lohani and Sereme 1989).

Increasing Resistance Levels through Selection

Susceptibility to downy mildew increases if a genetically uniform cultivar is grown extensively for several years on the same land. In the past, several pearl millet hybrids were withdrawn in India because over time, they became susceptible to downy mildew. However, research at ICRISAT Center showed that susceptible parents of some of these hybrids, inbred lines, and populations can be resurrected to high levels of resistance by selecting for resistance under high downy mildew pressure. This was demonstrated in a landrace from Chad (Singh et al. 1988) and also in 5141 A/B, the seed parents of hybrid BJ 104 (Singh 1983a). Lines thus selected showed high levels of downy mildew resistance at several locations in India. The reselected parental lines of BJ 104, (ICMA 841 and ICMP 84814) have much higher levels of downy mildew resistance than the original lines (5141A and J 104), while maintaining a high degree of phenotypic similarity to the original parents. The hybrid ICMH 84814, based on these reselected lines, is similar in yield and other phenotypic characteristics to BJ 104 (Singh et al. 1992). The male-sterile line, ICMA 841, is now a seed par-

ent of two hybrids, Pusa 23 and ICMH 423, which are under commercial cultivation in India (Singh et al. 1990).

Inheritance of Resistance

There are several reports on the inheritance of resistance to downy mildew. Generally, resistance was reported to be controlled by one or two dominant genes with some modifiers (Appadurai et al. 1975, Singh 1974, Gill et al. 1975, Gill et al. 1978), although there is one report indicating that resistance is a recessive trait (Singh et al. 1978). The information on the mode of inheritance is however, incomplete and unclear. This might be due to several reasons, such as the use of heterozygous parents in studies, use of variable pathogen populations, and unreliable screening techniques.

Management Strategies for the Control of Downy Mildew

The availability of resistant cultivars, an effective systemic fungicide for seed treatment, and some cultural practices provide good opportunities for the long-term management of this disease.

Diversification of Cultivars

Growing one hybrid for several years over a large area should be avoided. Instead, if hybrids are to be grown, several of them should be cultivated at the same time within a given area. Another approach to control downy mildew in hybrids would be to deploy genes over time, based on the principle of host-specificity (S.D. Singh, unpublished). As *S. graminicola* is highly host-specific, it is likely that the virulence of the oospore population of the pathogen will gradually shift to fit the genotype of the pearl millet cultivar grown every year in a given area for a long period. Conversely, the host-specific oospore population may die in 2–3 years, after the specific host variety is withdrawn from cultivation. This phenomenon has been observed with NHB 3, at a research station at Durgapura, Rajasthan (Singh and Singh 1987). However, if these approaches for hybrid cultivation are to work, a number of desirable hybrids are required, as is a coordinated effort by research programs, extension services, and seed production, distribution, and sales agencies.

Open-pollinated varieties, which are in fact populations in which genetic differences exist among plants, provide another opportunity to keep the disease under control. Due to their heterogeneity, such varieties will have a buffering effect against virulence shifts in the downy mildew pathogen. They are not likely to be disease free, but it is likely that disease epidemics will take a much longer time to develop on such cultivars. ICRISAT places major emphasis on open-pollinated varieties in India and in Africa. In Africa, where hybrids are not currently being grown for various reasons, open-pollinated cultivars would seem to be the most appropriate approach for the control of downy mildew in pearl millet.

The concept of topcross hybrids is one way to create genetic heterogenecity in F_1 hybrids. These hybrids are being produced at ICRISAT Center and may provide genetic variability that reduces vulnerability to downy mildew. Topcross hybrids may be especially appropriate in African countries where the downy mildew pathogen is both more variable and aggressive (Singh et al. 1992), and also in countries where seed production laws do not require any uniformity in growth and maturity.

Use of Recovery Resistance

Recovery resistance is a phenomenon in which systemically infected plants outgrow the disease and produce healthy panicles (Figs. 21a and b). This trait has been detected in many genotypes and has been increased

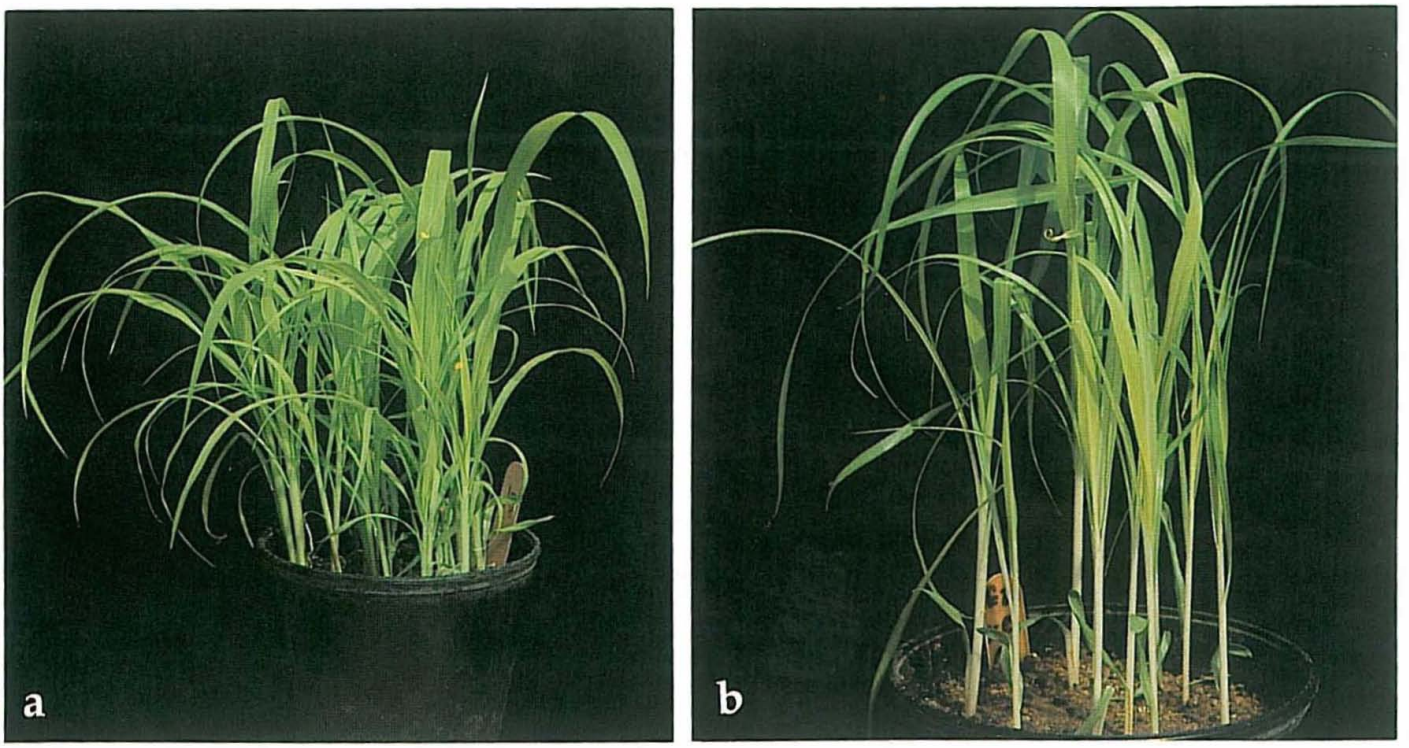

Figure 20. Two of the seven newly identified sources of resistance to downy mildew; (a) yellow seedlings, and (b) seedlings with white leaf sheath.

Resistant Cultivars Produced and Grown by Farmers

Four open-pollinated varieties developed at ICRISAT Center, WC-C75, ICMS 7703, ICTP 8203, and ICMV 155, have been released for cultivation in India. WC-C75 has been cultivated by Indian farmers since 1983, and has been grown annually in nine states on a total of over 1 million ha. There is no authentic report yet, of its resistance becoming ineffective, in contrast to the 'breakdown' of resistance of several hybrids in India during this period. In western Africa, ICRISAT has developed, in collaboration with Institut national d'études et de recherches agricoles (INERA), the national program in Burkina Faso, some promising downy mildew-resistant varieties such as IKMP 3, IKMP 2, and IKMV 8201 for widespread on-farm tests (Lohani and Sereme 1989).

Increasing Resistance Levels through Selection

Susceptibility to downy mildew increases if a genetically uniform cultivar is grown extensively for several years on the same land. In the past, several pearl millet hybrids were withdrawn in India because over time, they became susceptible to downy mildew. However, research at ICRISAT Center showed that susceptible parents of some of these hybrids, inbred lines, and populations can be resurrected to high levels of resistance by selecting for resistance under high downy mildew pressure. This was demonstrated in a landrace from Chad (Singh et al. 1988) and also in 5141 A/B, the seed parents of hybrid BJ 104 (Singh 1983a). Lines thus selected showed high levels of downy mildew resistance at several locations in India. The reselected parental lines of BJ 104, (ICMA 841 and ICMP 84814) have much higher levels of downy mildew resistance than the original lines (5141A and J 104), while maintaining a high degree of phenotypic similarity to the original parents. The hybrid ICMH 84814, based on these reselected lines, is similar in yield and other phenotypic characteristics to BJ 104 (Singh et al. 1992). The male-sterile line, ICMA 841, is now a seed par-

ent of two hybrids, Pusa 23 and ICMH 423, which are under commercial cultivation in India (Singh et al. 1990).

Inheritance of Resistance

There are several reports on the inheritance of resistance to downy mildew. Generally, resistance was reported to be controlled by one or two dominant genes with some modifiers (Appadurai et al. 1975, Singh 1974, Gill et al. 1975, Gill et al. 1978), although there is one report indicating that resistance is a recessive trait (Singh et al. 1978). The information on the mode of inheritance is however, incomplete and unclear. This might be due to several reasons, such as the use of heterozygous parents in studies, use of variable pathogen populations, and unreliable screening techniques.

Management Strategies for the Control of Downy Mildew

The availability of resistant cultivars, an effective systemic fungicide for seed treatment, and some cultural practices provide good opportunities for the long-term management of this disease.

Diversification of Cultivars

Growing one hybrid for several years over a large area should be avoided. Instead, if hybrids are to be grown, several of them should be cultivated at the same time within a given area. Another approach to control downy mildew in hybrids would be to deploy genes over time, based on the principle of host-specificity (S.D. Singh, unpublished). As *S. graminicola* is highly host-specific, it is likely that the virulence of the oospore population of the pathogen will gradually shift to fit the genotype of the pearl millet cultivar grown every year in a given area for a long period. Conversely, the host-specific oospore population may die in 2–3 years, after the specific host variety is withdrawn from cultivation. This phenomenon has been observed with NHB 3, at a research station at Durgapura, Rajasthan (Singh and Singh 1987). However, if these approaches for hybrid cultivation are to work, a number of desirable hybrids are required, as is a coordinated effort by research programs, extension services, and seed production, distribution, and sales agencies.

Open-pollinated varieties, which are in fact populations in which genetic differences exist among plants, provide another opportunity to keep the disease under control. Due to their heterogeneity, such varieties will have a buffering effect against virulence shifts in the downy mildew pathogen. They are not likely to be disease free, but it is likely that disease epidemics will take a much longer time to develop on such cultivars. ICRISAT places major emphasis on open-pollinated varieties in India and in Africa. In Africa, where hybrids are not currently being grown for various reasons, open-pollinated cultivars would seem to be the most appropriate approach for the control of downy mildew in pearl millet.

The concept of topcross hybrids is one way to create genetic heterogenecity in F_1 hybrids. These hybrids are being produced at ICRISAT Center and may provide genetic variability that reduces vulnerability to downy mildew. Topcross hybrids may be especially appropriate in African countries where the downy mildew pathogen is both more variable and aggressive (Singh et al. 1992), and also in countries where seed production laws do not require any uniformity in growth and maturity.

Use of Recovery Resistance

Recovery resistance is a phenomenon in which systemically infected plants outgrow the disease and produce healthy panicles (Figs. 21a and b). This trait has been detected in many genotypes and has been increased

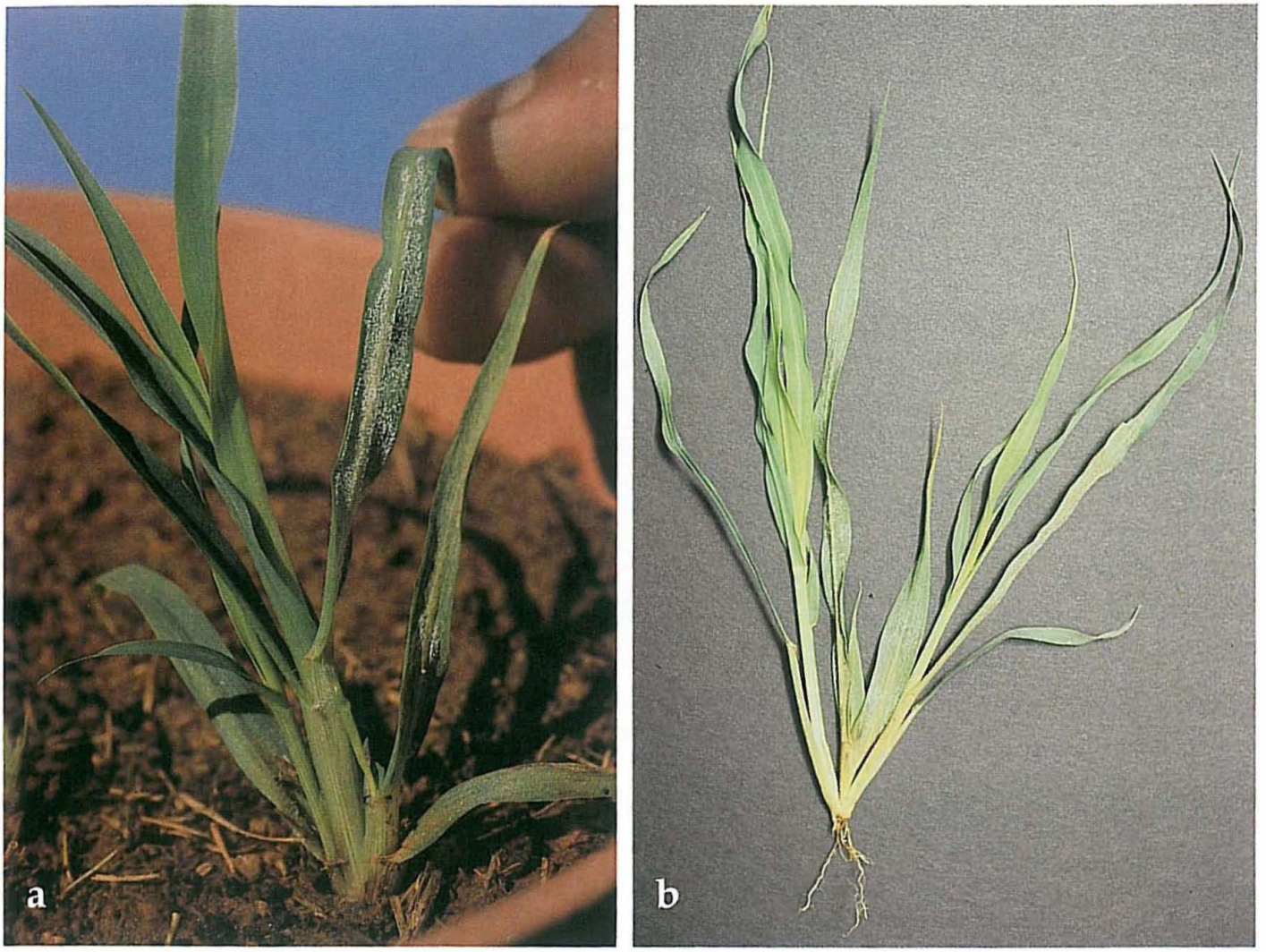

Figure 21. Natural remission of downy mildew symptoms (recovery) after the development of systemic infection. (a) Plant showing recovery on the same shoot; note the presence of asexual growth on several infected leaves. (b) Here the main infected shoot failed to recover, but the basal tillers that emerged were downy-mildew free.

through selection to a level where 95% of the plants showing downy mildew recover from the disease. Genotypes possessing this trait are not likely to interfere with the pathogen in germination, penetration, development of limited systemic infection and to a great extent in sporulation, thus allowing the pathogen to complete its life cycle and produce progenies. It is after these processes that the host outgrows the disease. This trait allows the host and the pathogen to coexist without affecting the yield (Singh and King 1988). Further, this trait is dominant over susceptibility. Thus in a hybrid combination, even if only one parent possesses this trait, the hybrid will have recovery resistance (Singh 1988).

The unique feature of cultivars with recovery resistance is that they are disease free in the absence of the disease, just like the traditionally resistant cultivars, but even in the presence of the disease, they quickly recover from disease and behave as resistant cultivars.

Use of Fungicides

Metalaxyl can be used effectively in some cases for the control of downy mildew of pearl

millet, but it should not be used excessively as such a practice is likely to encourage development of resistance to metalaxyl in *S. graminicola*. The best strategy would be to keep the fungicide in reserve, and use it only when the resistance breaks down unexpectedly and alternative resistance sources are not available (Singh and Shetty 1990a). Metalaxyl could also be of value in the production of quality seed (Singh and Shetty 1990b) for special situations.

Cultural Practices

Of the many known cultural practices, only roguing infected plants soon after their detection is strongly recommended. This should be done even if other control methods, including use of resistant cultivars, have been used. This operation will not only reduce the spread of the disease (in the same season by reducing sporangial production, or in the following season by reducing oospore production), but will also provide space for the surrounding plants to compensate for yield through increase in tillering.

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About ICRISAT

The semi-arid tropics (SAT) encompasses parts of 48 developing countries including most of India, parts of southeast Asia, a swathe across sub-Saharan Africa, much of southern and eastern Africa, and parts of Latin America. Many of these countries are among the poorest in the world. Approximately one sixth of the world's population lives in the SAT, which is typified by unpredictable weather, limited and erratic rainfall, and nutrient-poor soils.

ICRISAT's mandate crops are sorghum, pearl millet, finger millet, chickpea, pigeonpea, and groundnut; these six crops are vital to life for the ever-increasing populations of the semi-arid tropics. ICRISAT's mission is to conduct research which can lead to enhanced sustainable production of these crops and to improved management of the limited natural resources of the SAT. ICRISAT communicates information on technologies as they are developed through workshops, networks, training, library services, and publishing.

ICRISAT was established in 1972. It is one of 18 nonprofit, research and training centers funded through the Consultative Group on International Agricultural Research (CGIAR). The CGIAR is an informal association of approximately 50 public and private sector donors; it is co-sponsored by the Food and Agriculture Organization of the United Nations (FAO), the World Bank, and the United Nations Development Programme (UNDP).

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