Disease Analysis through Genetics and Biotechnology

INTERDISCIPLINARY BRIDGES TO IMPROVED SORGHUM AND MILLET CROPS

Edited by John F. Leslie and Richard A. Frederiksen

With a Foreword by Norman E. Borlaug

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John F. Leslie is associate professor, Department of Plant Pathology, Kansas State University.

Richard A. Frederiksen is professor, Department of Plant Pathology and Microbiology, Texas A&M.

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Variable Pathogens of Millets

S. B. King and R. P. Thakur

Introduction

'Millets' are a group of small-seeded cereal and forage grasses that are used for food, feed, and forage. They provide staple food for millions of people in arid and semi-arid tropical areas of the world, and some are also important in temperate zones. They are cultivated mostly in Asia, Africa, parts of Europe, and to a limited extent in the western hemisphere (primarily as forage). Grain from these crops is generally superior nutritionally to rice and wheat and has good storage qualities. Millets often provide the only cereal option for the marginal areas where they are grown. They are frequently short-term, warm season (summer) crops, and individual species or varieties frequently possess some unusual characters for adaptation, e.g. tolerance to or escape from drought, high temperature, low soil fertility, and diseases or pests, or use, e.g. special foods or beverages. Common and scientific names of species generally considered to belong to millets are given in Table 1.

In the past sorghum, and sometimes even maize, has been classified under the general term "millets". Production statistics often lump millets together, and figures sometimes include sorghum. Hence, it is difficult to obtain accurate production statistics for each species. Pearl millet is reportedly grown on about 27 million hectares worldwide with about 15 m ha in Africa, concentrated in the Sahelian and Northern Sudan Savanna

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S. B. KING: Eastern Africa Regional Cereals and Legumes Program (EARCAL), International Crops Research Institute for the Semi-Arid Tropics, P.O. Box 39063, Nairobi, Kenya; R. P. THAKUR: Cereals Program, International Crops Research Institute for the Semi-Arid Tropics, Patancheru, Andhra Pradesh 502 324, India.

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Table 1. Some common and scientific names of millets.

Common Name	Scientific Name
Pearl millet, bulrush millet, bajra	*Pennisetum glaucum* (L.) R. Br.
Foxtail millet, Italian millet	*Setaria italica* (L.) P. Beauv.
Proso millet, common millet	*Panicum miliaceum* L.
Finger millet, ragi	*Eleusine coracana* (L.) Gaertn.
Little millet	*Panicum sumatrense* Roth. ex. Roem. & Schult. (formerly *Panicum miliare*)
Kodo millet, ditch millet	*Paspalum scrobiculatum* L.
Japanese millet, barnyard millet	*Echinochloa crusgalli* (L.) P. Beauv.
Jungle rice, sawa millet	*Echinochloa colona* (L.) Link
Australian millet	*Echinochloa decompsitum*
Teff	*Eragrostis tef* (Zucc.) Trotter
Fonio millet, hungry rice	*Digitaria exilis* Stapf *Digitaria iburua* Stapf
Brown top millet	*Brachiaria (Panicum) ramosa* (L.) Stapf
Job's tears, adlay	*Coix lachryma-jobi* L.

zones stretching westward from central Sudan to the coast of Senegal, and 11 to 12 m ha in the Indian sub-continent, concentrated mainly in western and northwestern India [9]. About 0.5 m ha of pearl millet are grown annually in the southern and southeastern United States, mainly as a forage crop [8].

Collectively, the millets other than pearl millet probably occupy about 18-20 m ha worldwide. Distribution on a regional basis includes approximately 6.5 m ha in South Asia, 5 m ha in China, 4 m ha in the former USSR, and 3 m ha in Africa. Of these millets, finger millet is the main species grown in South Asia, followed in decreasing order by kodo, foxtail, little, proso, and barnyard millet. Foxtail and proso millets are the most important millet crops in China. Proso millet is grown extensively in the southern and southwestern, semi-arid regions of the former USSR. In Africa, finger millet is important in eastern Africa, especially

in the Lake Victoria region, and to a lesser extent in some countries of southern Africa. Teff is confined almost entirely to Ethiopia and Eritrea, where it is an important cereal. Fonio millet is grown in certain localities in western Africa, as is browntop millet. Some of these millets are grown to a limited extent in Europe and the United States [19].

Variable Pathogens

Diseases have been reported on virtually all of the millets [17,19]; however, pearl millet diseases have received by far the most research attention, followed probably by foxtail, finger, and proso millet. Literature on many of the millets is scanty, not readily available, and often not up to date. The few examples we found of variable pathogens of millets are given below.

Downy mildew of pearl millet. Downy mildew, caused by *Sclerospora graminicola* (Sacc.) Schroet., has been known for a long time as a disease of pearl millet in India and many African countries. *S. graminicola* has not been reported on pearl millet in the western hemisphere, although it occurs on *Setaria* spp. in the United States where it also was reported to infect maize under greenhouse conditions [14]. In India, there was little concern about downy mildew until disease epidemics developed on hybrids after their introduction to farmers in the late 1960s. Since that time, there have been several epidemics, and a number of new hybrids have been introduced and several, subsequently, have gone out of production due to increased levels of susceptibility to the disease [24]. With the introduction of more genetic diversity into the pearl millet hybrids grown in India, vulnerability to downy mildew has been reduced considerably from what it was a few years ago when hybrid options available to farmers were very limited. Resistance breakdown has not been a problem in Africa where land races are cultivated almost exclusively, except for some areas where heterogeneous varieties are also used. Resistance breakdown also may have been limited by sparse stands and low soil fertility.

There are numerous examples of the occurrence of variable pathotypes of *S. graminicola* in India where approximately 40% of the pearl millet crop is sown to hybrids [1,13,20,21,23,24]. These pathotypes have been detected largely on the basis of differential reactions using genetically uniform materials such as hybrids and inbreds [13,26]. In western Africa, where pearl millet production is still based almost entirely on land races and a few improved varieties, but not hybrids, pathogenic differences have been detected among geographically separated populations of *S. graminicola* [1,32]. Although pathogenic variation currently is not a problem for farmers in western Africa, researchers are concerned that the breeding and production strategies to be used be such that epidemics, such as those which occurred in India, can be avoided.

Michelmore et al. [15], working with Indian isolates, reported that *S. graminicola* is heterothallic with two compatible mating types. This finding implies that the pathogen has high genetic potential for producing new recombinants to create more variation in the population. Outbreeding and extensive variation within and between isolates from different geographical areas can be expected. This hypothesis was confirmed by Idris and Ball [11] who further demonstrated sexual compatibility between isolates from India and those from western Africa.

High genetic variability that leads to rapid selection and adaptation to new host genotypes was demonstrated in a recent study [28] where host genotype-specific virulence developed from a field population of the pathogen by selection through asexual generations. The influence of this selection through asexual generations varied for latent period and infection index in two pearl millet genotypes, a hybrid MBH 110 and an inbred 852B (Table 2). Selection for pathogenic fitness (latent period and infection index) was much faster on 852B than on MBH 110, probably indicating the nature and number of downy mildew resistance genes present in these two genotypes. These results also suggest that resistance and virulence (pathogenic fitness) in the pearl millet-downy mildew system are controlled by relatively few genes, but significant variations in virulence and aggressiveness were found among 10 single-oospore isolates of *S. graminicola* from ICRISAT Center on a set of resistant and susceptible genotypes [26].

In a recent study Thakur and Rao [unpublished] obtained highly significant effects of pathotype, host genotype, and host genotype x pathotype interaction for virulence and aggressiveness among five host genotype-specific pathotypes of *S. graminicola* on 14 pearl millet genotypes. These data indicate that differential host-pathogen interactions and distinct genetic groupings of pathotypes and host genotypes occur. High genetic variability for virulence accounts for the ability of the pathogen population to rapidly adapt to new, uniform host genotypes, such as F_1 hybrids [24].

Information on genetics of resistance to downy mildew is limited. In a collaborative study between ICRISAT and University College of North Wales, Bangor, UK, quantitative trait loci (QTL) mapping was done by screening F_4 progenies of two crosses involving genotypes resistant and susceptible to *S. graminicola* populations from Africa and India [3]. QTL mapping has revealed several QTLs (probably genes or their clusters) for resistance to Indian and African populations of the pathogen, each on different linkage groups. The QTLs found against the Nigerian pathogen population were on a different linkage group from those effective

Table 2. Effect of selection in asexual generations of *Sclerospora graminicola* for pathogenic fitness (latent period and infection index) on two pearl millet genotypes.

Sexual generation	Latent period[y]		Infection index[z]	
	MBH 110	852B	MBH 110	852B
1	10	7	13	83
2	10	7	18	61
3	10	6	25	108
4	7	5	41	129
5	7	5	31	147
6	7		55	
7	6		69	
8	5		110	
9	6		81	
10	5		84	
11	5		51	
12	5		90	

[y] Latent period in days - the time between inoculation and symptom appearance with sporulation.

[z] Infection index calculated as the ratio between arc-sine transformed values of percentage infection on MBH 110/852B and the highly susceptible genotype 7042S multiplied by 100.

against Indian isolates. Two QTLs were found against the Niger and Mali pathogen populations, one was the same as that found against the Nigerian population and one was different from those found against either the Nigerian or Indian populations. These results indicate the potential usefulness of molecular marker techniques in the identification of resistance genes and their strategic utilization in resistance breeding.

Rust of pearl millet. There is some evidence for pathogenic variability in *Puccinia substriata* var. *indica* (= *Puccinia penniseti* Zimm.). Ramakrishnan and Sundaram [18] reported two races of this pathogen on the basis of color, associated necrosis, and distribution of uredinia on leaves. These differences were maintained through serial transfers, but no differences in virulence were noted between the two types when inoculated onto a series of pearl millet lines and varieties. Only one type, however, was able to produce uredinia after inoculation on crosses between pearl millet and *Pennisetum pupureum* (elephant grass or napier grass). Basu-Chaudhary and Sinha [2] found slight pathogenic differences among isolates of the pathogen from four distinct pearl millet growing areas of India when a set of pearl millet lines were inoculated. However, in another test in India involving different sets of the host and pathogen, no pathogenic differences were observed [6]. Similarly, no evidence for pathogenic variation was found during 11 years of multilocational testing in India with the ICRISAT coordinated International Pearl Millet Rust Nursery (IPMRN) [10].

Pathogenic variation was found, however, when 10 pearl millet lines were inoculated with 12 collections of the rust pathogen from India, Tanzania, Zimbabwe, Senegal, and the United States [S.B. King, unpublished]. The rust resistant line 85DB, whose resistance is based on a single dominant gene obtained from *P. glaucum* ssp. *monodii* from Senegal [7], was resistant to all isolates except the two from Senegal. This reaction difference was noted on leaves inoculated at the seedling stage and those inoculated shortly after flowering. ICML 11, a pearl millet line whose resistance is also based on a single dominant gene, showed resistance in multilocational tests in India [22], but it is reportedly susceptible in Georgia, U.S.A. [W.W. Hanna, personal communication].

Although there seems to be little doubt that pathogenic variation exists in the pearl millet rust pathogen, this variability has not yet presented a problem for pearl millet cultivation.

Ergot of pearl millet. There have been a few reports of small differences in virulence among isolates of *Claviceps fusiformis* Loveless, causal agent of ergot in pearl millet [25]. However, the data do not show clear evidence for pathogenic variability, although morphological differences including differences in sclerotial size have been reported among isolates of the ergot pathogen [5]. Ten years of multilocational testing in India and some countries of western Africa through the International Pearl Millet Ergot Nursery (IPMEN) did not suggest physiologic specialization in the ergot pathogen [29].

There is no evidence that variability in the ergot pathogen is a constraint to pearl millet production. Resistance to *C. fusiformis* in pearl millet is basically conferred by an escape mechanism favored by rapid pollination and short protogyny [27]. A constriction that develops in stylodial tissue after passage of the pollen tube may also contribute to resistance [33]. It seems unlikely that pathogenic variation if it developed would easily overcome this type of resistance mechanism.

Smut of pearl millet. There is no convincing evidence for pathogenic variation among isolates of the smut pathogen, *Tolyposporium penicillariae* Bret. [=*Maesziomyces penicillariae* (Bref.) Vanky]. As with the ergot pathogen, 10 years of multilocational testing in India and western Africa has not provided evidence for pathogenic variation [30], although Chahal et al. [4] did report finding one isolate of the smut pathogen that was more virulent than other isolates. However, pathogenic variability has not been reported as a field problem in pearl millet smut.

Head smut of proso millet. In the Volga region of the former Soviet Union, there has been a breeding program to control head smut [*Sphacelotheca destruens* (Schelecht.) Stevenson & Johnson], apparently a serious problem of proso millet in that area. The resistance breeding program has relied heavily on single dominant genes. At least three physiologic races of the pathogen have been reported and cause a production problem [12].

Conclusions

Based on a review of the literature available to us, pathogen variability is known to cause a field problem in only two (downy mildew of pearl millet and head smut of proso millet) of the five diseases in which variability has been reported. Conclusive evidence for pathogenic variability has been shown for rust of pearl millet, but this variability has not yet developed into a field problem, and the case for pathogenic variability in pathogens of ergot and smut diseases of pearl millet is weak. However, in considering the diseases reported on millets, many, e.g. rusts, smuts, and downy mildews, involve pathogens that are characteristically variable on other crops. Rust and smut diseases have been reported on almost all the millets, and downy mildew diseases occur on about half of them. Leaf blight pathogens belonging to genera of *Bipolaris*, *Drechslera*, or *Helminthosporium* are also reported on almost all the millets. Furthermore, the pathogen, *Pyricularia grisea*, or closely related species, commonly occur on several millets. Blast disease caused by *P. grisea* is a serious problem of finger millet in almost all production areas in Asia and Africa. Their is no evidence for pathogenic variability in *P. grisea* on finger millet, although the immense capability of *P. grisea* for variability on rice in the rice blast disease has been well known for a long time [16,31].

One might wonder, therefore, why there has not been a greater expression of variability on the millets by these pathogens? We believe there may be several factors responsible for the apparent homogeneity. Certainly it is possible that variability is present but has not yet been detected due to the relatively low status of these crops in research and in world trade. Secondly, the fact that these crops have received so little attention in crop improvement relative to other crops, including other cereals, may also be an important factor limiting the development and expression of variable pathogens. Thirdly, millets are currently grown in marginal environments largely as land races that are heterogeneous populations. The development of physiologic races of pathogens is generally favored by continuous and widespread use of genetically uniform cultivars which exert selection pressure on pathogen populations to produce variants that are compatible with the host. An example of such an occurrence in millet is the development of destructive pathotypes of *S. graminicola* on pearl millet in India after the widespread adoption of hybrids.

Research on variability in the downy mildew pathogen of pearl millet, including the application of biotechnology, should be encouraged because of the magnitude of this disease problem and the good prospects for successfully developing gene-based control measures. There may also be good cause for applying biotechnology to control the problem of pathogen variability in head smut of proso millet. However, research on variability in pathogens causing other diseases of the millets probably remains a relatively low priority, at least for the foreseeable future.

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Plant Disease Control in Sorghum and Pearl Millet

R. R. Duncan and W. A. J. de Milliano

Sorghum [*Sorghum bicolor* (L.) Moench] and pearl millet [*Pennisetum glaucum* (L.) R.Br.], are grown for their grain, stems, and total biomass. The grain is used in different food preparations, for local and commercial brewing, malted and fermented foods, composite flour, starch production, and for feed either directly or in concentrates [39,93]. The stems and biomass are used for local construction purposes, fencing, livestock feed, or forage [29 108]. From the sorghum sweet stems, various industrial products are made, such as sugar, syrup and ethanol [39]. Sorghum is grown particularly in areas with high temperature and low rainfall, throughout Africa, Asia, the Americas and Australia [39]. Pearl millet is the most drought avoiding of all domesticated cereals, and is the principal foodcrop in parts of Africa and India [30]. As the uses for these crops diversify, the demand will increase for stable cultivars with high yield and resistance to important pests and diseases. The crops are indispensable for survival of man and domesticated animals in austere, dry environments [46]. Improvements in productivity may alleviate the requirement to increase production areas, and hopefully will provide an incentive to culture the fields with minimal soil deterioration on a sustainable basis.

Sorghum and pearl millet have had many diseases in the past [96, 110] and still have today [29,39,128]. Disease control will stabilize and even increase yields. With Doggett's hypothesis in mind, that the importance of diseases is positively correlated with yield [128], disease control

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R. R. DUNCAN: Department of Crop and Soil Sciences, 1109 Experiment Street, University of Georgia, Griffin, Georgia 30223-1797; W. A. J. DE MILLIANO: Technology Department, S & G Sandoz Seeds, Postbus 26, 1600 AA Enkhuizen, The Netherlands.

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