Sources of Resistance to Downy Mildew in Wild and Weedy Sorghums

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ABSTRACT

Sorghum downy mildew (SDM), caused by *Peronosclerospora sorghi* Weston and Uppal (Shaw), is a serious disease of sorghum [*Sorghum bicolor* (L.) Moench] and maize (*Zea mays* L.). The wild relatives of sorghum, both cross compatible and cross incompatible with *S. bicolor*, could provide alternate sources of resistance genes for the long-term control of SDM. The objective of this study was to assess the downy mildew reaction of several taxa of wild and weedy sorghums. One hundred three wild and weedy sorghums, and six cultivated types belonging to five sections, representing 17 species, originating from Asia, Australia, Africa, and the USA, were greenhouse tested for downy mildew resistance during the rainy seasons of 1998 and 1999 at ICRISAT, Patancheru, India. Forty-five accessions comprising 15 species from four sections, parasorghum, heterosorghum (*S. laxiflorum* Bailey), chaetosorghum (*S. macrospermum* Garber), and stiposorghum (*S. angustum* S. T. Blake, *S. ecarinatum* Lazarides, *S. extans* Lazarides, *S. intrans* F. Muell. ex Benth., *S. interjectum* Lazarides, *S. stipoideum* (Ewart & Jean White) C. Gardener & C. E. Hubb.), including all accessions from Australia, exhibited immunity to downy mildew. Cultivated types and wild races of section Sorghum showed the greatest susceptibility (mean downy mildew infection of 62 and 46%, respectively), while accessions of *S. halepense* (L.) Pers. were comparatively less susceptible (36% mean downy mildew infection). Potential new sources of resistance genes from wild and weedy sorghums were identified that could be used to develop resistant cultivars to control downy mildew.

SORGHUM DOWNY MILDEW is a serious disease of sorghum and maize and causes heavy losses in grain yield in many parts of the semi arid tropics where sorghum is a staple for human and animal consumption. The disease is of quarantine significance because of its seed-borne nature. A number of sources of resistance have been identified and successfully used to produce disease resistant cultivars (Frederiksen et al., 1973, Henzell et al., 1982, Shivana and Anahosur, 1990). However, the breakdown of resistance due to the development and spread of more virulent races of the pathogen associated with the repeated cultivation of resistant cultivars underscores the need to develop cultivars with broad-based resistance utilizing genes from diverse sources (Craig and Odvody, 1992).

Wild species have contributed novel resistance genes to the improvement of cereals such as rice (*Oryza sativa* L.), wheat (*Triticum aestivum* L.), and barley (*Hordeum vulgare* L) (Goodman et al., 1987). The wild relatives of sorghum, both cross compatible and cross incompatible with *S. bicolor*, could provide alternate sources of resistance genes for the long-term control of SDM. The objective of this study was to assess the downy mildew reaction of several taxa of wild and weedy sorghums.

MATERIALS AND METHODS

One hundred nine sorghum accessions, belonging to 17 species including five accessions of an unknown species, representing five sections, were screened for their reaction to SDM. Species of sections chaetosorghum, heterosorghum, and stiposorghum were represented by 19 accessions exclusively from Australia. Section parasorghum was represented by 28 accessions belonging to five species from Australia [*S. australiense* Garber and Snyder, *S. brevicallosum* Garber, *S. timorense* (Kunth) Buse, *S. nitidum* (Vahl) Pers. and *S. matarankense* Garber and Snyder], one species from Africa (*S. versicolor* Anderss.), and one species from Africa and Asia [*S. purpureosericeum* (Hochst. Ex A. Rich.)]. Section sorghum was represented by 13 accessions of weedy S. halepense from Asia, Africa, and the USA, and 43 accessions of four wild races of *S. bicolor* subsp. *verticilliflorum* from Africa and the USA. Six cultivated types (*Sorghum bicolor* subsp. *bicolor*) including a commercial hybrid were selected at random to represent the five races. The accessions were chosen at random from the sorghum collection maintained at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT). The experiments were conducted during the 1998 and 1999 rainy seasons at ICRISAT, Patancheru, Andhra Pradesh, India.

The pathogen culture being maintained at ICRISAT was used in the screening. The pathogen was multiplied on an SDM susceptible cultivar, DMS 652 (IS 18433), grown in pots. The pots were maintained under greenhouse conditions at $28 \pm 2°C$. Seeds of wild and cultivated accessions were presoaked for 3 h and incubated at 25°C. in the dark. Cultivated types germinated in 24 h, while wild accessions took 2 to 3 d. About 25 sprouted seeds of similar shoot and root lengths were transplanted in 15-cm-diam pots filled with a mixture of black soil (vertisol) and farm yard manure. Each accession was replicated twice. Seedlings at the coleoptile stage to one-leaf stage were inoculated with conidia (a suspension with 4×10^5 conidia mL^{-1}) as described by Reddy et al. (1992). The susceptible, DMS 652 (IS 18433), and the resistant, QL 3 (IS 18757), cultivars were included as controls. After inoculation, the pots were incubated at 20°C and 95% RH overnight, and then transferred to the greenhouse for disease development. Symptoms of systemic infection with clear chlorosis beginning at the base of the infected leaves started to appear 8 to 12 d after inoculation, and were clearly visible at about 14 d. Counts of total plants and infected plants were recorded at 14 and 21 d after inoculation and percentage of diseased plants (disease incidence) was calculated. Accessions that remained disease free were reinoculated to ensure that these were not escapes.

The experiment was conducted in a completely randomized design. The check cultivars (controls) were replicated five times. The test entries differed in the two years. Percentage infection data were analyzed by the REML (Residual Maximum Likelihood) procedure that assumed a fully random model after angular transformation. The REML analysis was preferred since it can be used to provide unbiased and efficient estimates of treatment effects in unbalanced designs with more than one source of error. It also allows the assessment

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Table 1. Reaction of sorghum accessions to sorghum downy mildew (SDM) under greenhouse conditions.

Section	Species/subspecies/race	Country of origin	Accession identity	Mean SDM incidence (%)†
Sorghum	*S. bicolor* subsp. *bicolor*:			
	race guinea	Zimbabwe	IS 14383	0
	race kafir	USA	IS 18773	43.5
	race caudatum	Sudan	IS 21812	71.8
	race durra	India	IS 12868	87.6
	race bicolor	USA	IS 611	90
	hybrid		CSH1	76.67
	S. bicolor subsp. *verticilliflorum race aethiopicum*	Egypt	IS 18821	0
		Cameroon	IS 27584	10.2
		Sudan	IS 18819	30.7
		Sudan	IS 14564	51.1
		Sudan	IS 14567	75.5
	S. bicolor subsp. *verticilliflorum race arundinaceum*	USA	IS 18882	0
		Ivory Coast	IS 18826	3.1
		Malawi	IS 18833	10.5
		Tanzania	IS 18830	13.4
		Ivory Coast	IS 18824	15.9
		Malawi	IS 14359	20.5
		Nigeria	IS 18878	32.4
		South Africa	IS 14301	45
		USA	IS 18823	45.4
		Angola	IS 14216	50
		Angola	IS 14211	60.7
		Angola	IS 20889	69.5
		Burundi	IS 31540	72.1
		Ghana	IS 18883	72.2
	S. bicolor subsp. *verticilliflorum race verticilliflorum*	Ethiopia	IS 14583	21.6
		Ethiopia	IS 18873	31.3
		Kenya	IS 20995	31.4
		South Africa	IS 14278	34.4
		Malawi	IS 14357	35.1
		South Africa	IS 14313	65.7
		Chad	IS 18802	70.0
		Sudan	IS 18865	72.5
		Angola	IS 14219	76.2
		Ethiopia	IS 14719	77.3
		Kenya	IS 14571	82.2
		Angola	IS 14259	84.4
		Angola	IS 14234	86.7
		USA	IS 18875	90.6
		Ethiopia	IS 14717	91.6
	S. bicolor subsp. *verticilliflorum race virgatum*	Egypt	IS 18813	1.7
		Egypt	IS 18810	1.8
		Somalia	IS 32754	26.9
		Egypt	IS 18809	30.7
		Egypt	IS 18808	32.1
		Somalia	IS 32755	48.2
		Sudan	IS 18817	49.1
		Egypt	IS 18805	65.6
		USA	IS 18803	100.0
	S. halepense	Sudan	IS 33712	0
		Angola	IS 14241	8.8
		India	IS 18849	16.8
		South Africa	IS 18926	18.8
		USA	IS 18897	21.1
		India	IS 18847	28.5
		USA	IS 18899	31.7
		India	IS 18850	32.2
		Angola	IS 14212	44.0
		India	IS 18845	49.5
		Angola	IS 14263	57.3
		USA	IS 18891	62.4
		South Africa	IS 14299	94.2
Chaetosorghum	*S. macrospermum*	Northern Territory, Australia	PQ24	0
Heterosoghum	*S. laxiflorum*	Northern Territory, Australia	PQ155	0
		Northern Territory, Australia	PQ156	0
		Northern Territory, Australia	PQ157	0
		Northern Territory, Australia	PQ158	0
		Queensland, Australia	PQ159	0
		Queensland, Australia	PQ162	0
		Australia	IS 18958	0

Table 1. Continued.

Section	Species/subspecies/race	Country of origin	Accession identity	Mean SDM incidence (%)†
Parasorghum	S. australiense	Australia	IS 18954	0
		Australia	IS 18955	0
		Australia	IS 18956	0
	S. brevicallosum	Northern Territory, Australia	PQ2/1	0
		Australia	RN320	0
	S. matarankense	Northern Territory, Australia	PQ25	0
		Australia	RN341	0
	S. nitidum	Queensland, Australia	PQ22-1	0
	S. purpureosericeum subsp. deccanense	India	RN285	0
		Tanzania	IS 18943	0
		India	IS 18947	0
		India	IS 22191	0
		India	IS 18951	3.1
	S. purpureosericeum subsp dimidiatum	Sudan	IS 18944	0
		Sudan	IS 18945	0
	S. timorense	Northern Territory, Australia	PQ14-1	0
		Northern Territory, Australia	PQ26-1	0
	S. versicolor	South Africa	IS 18926	0
		Angola	IS 14262	0
		South Africa	IS 14275	0
		South Africa	IS 18940	0
		Tanzania	IS 18941	0
		Tanzania	IS 23177	3.2
	S. sp	Malawi	IS 18929	0
	S. sp	Tanzania	IS 23147	0
	S. sp	Tanzania	IS 23159	0
	S. sp	Tanzania	IS 23175	0
	S. sp	Tanzania	IS 18942	0
Stiposorghum	S. angustum	Queensland, Australia	PQ10	0
		Queensland, Australia	PQ2	0
		Queensland, Australia	PQ3	0
		Queensland, Australia	PQ5	0
		Queensland, Australia	PQ7	0
		Queensland, Australia	PQ9	0
	S. ecarinatum	Northern Territory, Australia	PQ19	0
	S. extans	Northern Territory, Australia	PQ35	0
	S. intrans	Northern Territory, Australia	PQ30	0
	S. interjectum	Australia	PQ47	0
	S. stiposorghum	Western Australia, Australia	PQ100	0

† Mean SDM incidence on resistant and susceptible controls was 0 and 85%, respectively; Mean over all the accessions was 25.89%: SE: ±2.59.

of information over similar experiments conducted at different times or places. Assuming asymptotic normality, the ratio of the estimated variance component to its standard error was compared with Z (standard normal deviate) table values at the 5 and 1% levels and error probabilities to test statistical significance of the effect of the variance components. The predicted mean values obtained were retransformed by inverse angular transformation.

RESULTS AND DISCUSSION

Highly significant ($P < 0.01$ level) differences in resistance to downy mildew were observed among the 109 accessions (Table 1). No significant accession × year or year effects were found. Forty-five of the wild accessions belonging to sections heterosorghum, chaetosorghum, stiposorghum, and parasorghum remained downy mildew free. Whereas, two accessions of parasorghum, IS 18951 (*S. purpureosericeum*) and IS 23177 (S. versicolor), developed about 3% downy mildew. Among the wild and weedy types in section sorghum, three accessions, one each in races *aethiopicum* (IS 18821) and *arundinaceum* (IS 18882) and one accession of *S. halepense* (IS 33712) were free from downy mildew. Accessions of race *verticilliflorum* showed the highest susceptibility (mean disease incidence of 63.4%), while those of race *aethiopicum* were less susceptible (mean downy

mildew of 33%). Range of disease incidence in different accessions of race *virgatum* varied from 1.7 to 100%.

The six accessions of cultivated sorghum showed a high level of disease incidence (mean downy mildew of 62%) ranging from 43.5 to 90%, except IS 14383. IS 14383, a cultivated guinea sorghum from Zimbabwe, remained downy mildew free in successive inoculation tests. However, when screened by the sandwich test, two of the 42 inoculated plants developed downy mildew but the seedlings subsequently recovered within 15 d. This accession grew to a height of 2.25 m during the post rainy season at the ICRISAT center, flowered in 58 d, and produced lustrous (shiny) grain.

A large proportion of wild and weedy accessions (52%) remained either downy mildew free or developed less than 10% disease to the ICRISAT pathotype. These sorghums, particularly those belonging to parasorghum, heterosorghum, chaetosorghum, and stiposorghum possess rich sources of genetic resistance to downy mildew. However, there is a need to test these accessions to other populations of the pathogen (Craig and Frederiksen, 1980; Pawar et al., 1985) to identify sources with broad-spectrum resistance. Such a screening will also be useful in determining differential susceptibilities of different sorghum species as has already been reported (Bonman et al., 1983).

Freedom from downy mildew in all the accessions

from Australia compared with large variations (0–100% downy mildew) in the downy mildew reaction of accessions from other countries is of considerable interest. Since downy mildew on sorghum is not prevalent in Australia, barring a few reports of its occurrence in maize (Reddy, 1979), the resistance in these accessions appears to have evolved in the absence of the pathogen and plausibly occurs by the presence of secondary metabolites inimical to pathogen growth. However, these are not isolated instances since resistance has also been detected in a cultivated sorghum cultivar (QL3) from Australia (Williams et al., 1982). The resistance in QL 3 has been effective against 16 pathotypes of downy mildew (Pawar et al., 1985).

The resistant accessions among the wild races of section sorghum noted in this study are primarily from East Africa (Sudan and Egypt). IS 18882, the resistant *arundinaceum*, though listed in the records as being from USA, in all probability was also originally from Africa. The north-east quadrant of Africa being the center of domestication and primary center of diversity of cultivated sorghums, the region is likely to harbor diversity to disease resistance as has been demonstrated for other crops (Leppik, 1970).

With the availability of resistance in the wild and weedy types, it is important to determine the degree of diversity among the downy mildew resistance genes in different accessions from Australia and also from other parts of the world. This study could provide information on the uniqueness (or lack thereof) of resistance genes in wild and weedy sorghums. If these accessions possess different genes, then it makes a strong case to use particularly the cross-compatible types to produce cultivars with durable resistance for areas where downy mildew is a serious problem and breakdown of resistance occurs. This approach is likely to provide long-term control of this disease as has been shown in other instances (Goodman et al., 1987).

Development of downy mildew symptoms on the cultivated sorghum IS 14383 after forced inoculation (sandwich test) and its subsequent recovery is quite remarkable. This phenomenon of recovery resistance has been reported earlier in pearl millet (*Pennisetum americanum* L) and sorghum (Singh and King, 1988; Singh and de Milliano, 1989). While IS 14383 could be a valuable source of downy mildew resistance, its uniqueness needs to be characterized in terms of tangible metabolites, possibly the prevalence of phenolics. There is also a need to test its reaction to other pathotypes. The present study identifies many new sources of resistance to sor-

ghum downy mildew from cross compatible species of *Sorghum*, which could be used to develop resistant cultivars. Recent advancements in genetic engineering offer a distinct possibility of utilizing genes from cross-incompatible species as well.

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