VIRULENCE DIVERSITY IN NORTH INDIAN ISOLATES OF *SCLEROSPORA GRAMINICOLA*, THE PEARL MILLET DOWNY MILDEW PATHOGEN

R. Sharma[1], V.P. Rao[1], S. Senthilvel[1], S.C. Rajput[2] and R.P. Thakur[1]

[1] *International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, 502324 Hyderabad, Andhra Pradesh, India*
[2] *Regional Research Station, Chandra Shekhar Azad University of Agriculture and Technology, 202125 Kalai, Aligarh, Uttar Pradesh, India*

SUMMARY

On-farm surveys were conducted in the Uttar Pradesh (India) during the two rainy seasons 2007 and 2008 to monitor pearl millet (*Pennisetum glaucum*) downy mildew incidence. Twenty-one isolates of *Sclerospora graminicola*, the pearl millet downy mildew pathogen, were collected from different hybrid cultivars. These isolates were established on seedlings of the highly susceptible line 7042S grown in the greenhouse and were characterized for their virulence diversity using a set of seven host differential lines. Quantitative differences in virulence among pathogen isolates were determined by calculating virulence index (percent disease incidence × latent period^{-1}). Results were submitted to cluster analysis using the Average Linkage method to determine similarity among pathogen isolates. The two highly virulent isolates, Sg 492 from Aligarh and Sg 510 from Badaun, representing geographically diverse locations were selected for use in greenhouse screening of pearl millet breeding lines.

Key words: *Sclerospora graminicola*, downy mildew, pearl millet, virulence, pathotype, breeding.

INTRODUCTION

Downy mildew (DM) caused by *Sclerospora graminicola* is an important disease of pearl millet [*Pennisetum glaucum* (L.) R. Br.]. The disease is highly destructive and widespread in the major pearl millet-growing areas of the world (Williams, 1984; Jeger *et al*., 1998). In India, the disease is quite severe on single-cross F_1 hybrids and causes substantial yield losses. *S. graminicola* is largely heterothallic and has a rapid asexual generation cycle, thus it can produce millions of spores in a short time (Idris and Ball, 1984; Michelmore *et al*., 1982). Existence of mating types and their frequency greatly contributes towards the development of new recombinants in the pathogen populations (Pushpavathi *et al*., 2006a). These characteristics help the pathogen to produce new variants with changed virulence that can be selected on resistant cultivars. Pathogen populations with new virulence genes could arise either because of sexual recombination/mutation or because of gene flow. Evolution of host-specific virulences in pearl millet downy mildew is well documented (Thakur *et al*., 1992; Sastry *et al*., 2001; Pushpavathi *et al*., 2006b), as a result of which resistant genotypes lose their effective resistance within a short period, leading to the development of new pathotypes/races in the pathogen populations (Kolmer *et al*., 2006).

Pathogenic variability in *S. graminicola* studied through a collaborative International Pearl Millet Downy Mildew Virulence Nursery has revealed differences in *S. graminicola* populations at different locations, including those within India (Thakur *et al*., 2004, 2006; Rao *et al*., 2005). The on-farm DM surveys during 1994-2004 in the hybrid-intensive states of Maharashtra, Rajasthan, Gujarat, and Haryana revealed increased DM susceptibility of a hybrid when grown in the same field for more than three consecutive crop seasons, indicating the emergence of a pathotype with new/changed virulence (Thakur *et al*., 2003; Rao *et al*., 2005). Therefore, pathogen populations in the major crop-growing areas need to be periodically monitored and characterized to identify new pathotypes in the target area. Virulence change in *S. graminicola* populations is monitored through on-farm surveys for downy mildew incidence and by characterizing pathogen isolates for virulence diversity. Studies done at ICRISAT and elsewhere have shown large pathogenic variability of *S. graminicola* populations from India and other countries (Shivaramakrishna *et al*., 2003; Thakur *et al*., 2004; Sharma *et al*., 2010).

S. graminicola isolates from the major pearl millet-growing areas of India have been characterized and the most virulent pathotypes from different regions are being maintained at ICRISAT for greenhouse screening of breeding material. However, pathogen populations from Uttar Pradesh, the fourth largest pearl millet producing state (about 0.9 million ha annually) in India, have not yet been characterized.

This study aimed at determining the variability in pathogenicity (ability of a pathogen isolate to cause

Corresponding author: R. Sharma
Fax: +91.30713074
E-mail: r.sharma@cgiar.org

>10% DM incidence) and virulence (high DM incidence and low latent period in the differentials) among *S. graminicola* populations by means of reaction of pathogen isolates on host differentials and identification of virulent pathotypes of the fungus for use in the screening of pearl millet hybrid parent lines targeted for development of hybrids suited for cultivation in the northern plains in India.

MATERIALS AND METHODS

DM survey and collection of isolates. The surveys were conducted to monitor DM severity in fields of eight districts of Uttar Pradesh during the rainy seasons 2007 and 2008 when the crop was at the preboot to flowering stages. During the survey, one pearl millet field was sampled at approximately every 10 km along the roadside, depending on crop intensity and hybrid diversity. In each field (≈ 0.4 ha), 5 random subplots (4 subplots at the corners and one in the center) were selected and within each subplot a minimum of 50 plants were visually checked in 2-3 rows for DM symptoms. Percent disease incidence was calculated for each field as total diseased plants/total observed plants x 100.

Twenty-one samples, collected from DM-infected leaves as sporangial isolates, came from six highly susceptible hybrids, hybrids of unknown identity, and local cultivars from seven Uttar Pradesh districts (Aligarh, Badaun, Bulandshehar, Etah, Hathras, Mathura and Moradabad) (Table 1, Fig. 1). Two isolates Sg 298 (from New Delhi) and Sg 334 (from Bhiwani, Haryana), the two neighboring states of Uttar Pradesh, collected during 1999 and 2001 surveys, respectively, and being presently used at ICRISAT for greenhouse screening of pearl millet breeding lines targeted for northern plains, were included in the study as reference isolates. These isolates were maintained through asexual generations in isolation chambers in the greenhouse on ICMP 451, 841 B, W 504-1 and 7042S seedlings.

Virulence diversity. *Host differentials.* Seven pearl millet genotypes P 7-4, P 310-17, 700651, 7042R, IP 18292, IP 18293 and 852B exhibiting differential reaction in the International Pearl Millet Downy Mildew Virulence Nursery (Thakur *et al*., 2004), and two known DM susceptible lines (ICMP 451 and 7042S) were selected as host differentials for variability studies.

Inoculum preparation and inoculation. Sporangial inocula of the 23 isolates were raised on seedlings of the highly susceptible genotype 7042S in isolation chambers in a greenhouse at ICRISAT. Sporangia from sporulating leaves were harvested in ice-cold water and the spore concentration was adjusted to 1×10^6 ml^{-1}. Pot-grown seedlings of the differential lines were spray-inoculated at the coleoptile stage using an atomizer. Inoculated seedlings were incubated at 20ºC and >90% relative humidity (RH) for 20 h, then transferred to greenhouse benches maintained at 25±2°C and >95% RH for disease development for the next 2 weeks. The experiment

Table 1. *Sclerospora graminicola* isolates collected in Uttar Pradesh.

Isolate	Year	Cultivar	Location
Sg 482	2007	Pioneer 86M32	Bedai Sadabad, Hathras
Sg 483	2007	Kaveri 456	Chandola sujampur, Aligarh
Sg 489	2007	GK 1044	Bahidpur Kasgunj, Etah
Sg 490	2007	Pioneer 86M32	Bhudia, Aligarh
Sg 491	2007	Pusa 383	Kalai, Aligarh
Sg 492	2007	Pioneer 86M32	Iglas, Aligarh
Sg 493	2007	Pioneer 86M32	Sathini Aligarh
Sg 494	2007	Pioneer 86M32	Perusuva Mott, Mathura
Sg 506	2008	Pioneer 86M32	Koyal Mat, Mathura
Sg 507	2008	Krishna	Ira, Mathura
Sg 508	2008	Hybrid	Jamunanagar, Bulandshahr
Sg 509	2008	Local	Beechpuri, Badaun
Sg 510	2008	Hybrid	Gannur, Badaun
Sg 511	2008	Hybrid	Duvari, Badaun
Sg 512	2008	Local	Berpur, Badaun
Sg 513	2008	Hybrid	Ganeshpur, Badaun
Sg 514	2008	Hybrid	Baagwala, Badaun
Sg 515	2008	Hybrid	Baburata, Moradabad
Sg 516	2008	Local	Narora, Buladshahr
Sg 517	2008	Hybrid	Salari, Bulandshahr
Sg 518	2008	Pioneer 86M32	Nanglababu, Hathras
Sg 298	1999	W 504-1	New Delhi
Sg 334	2001	Hybrid	Neemriwali, Bhiwani, Haryana

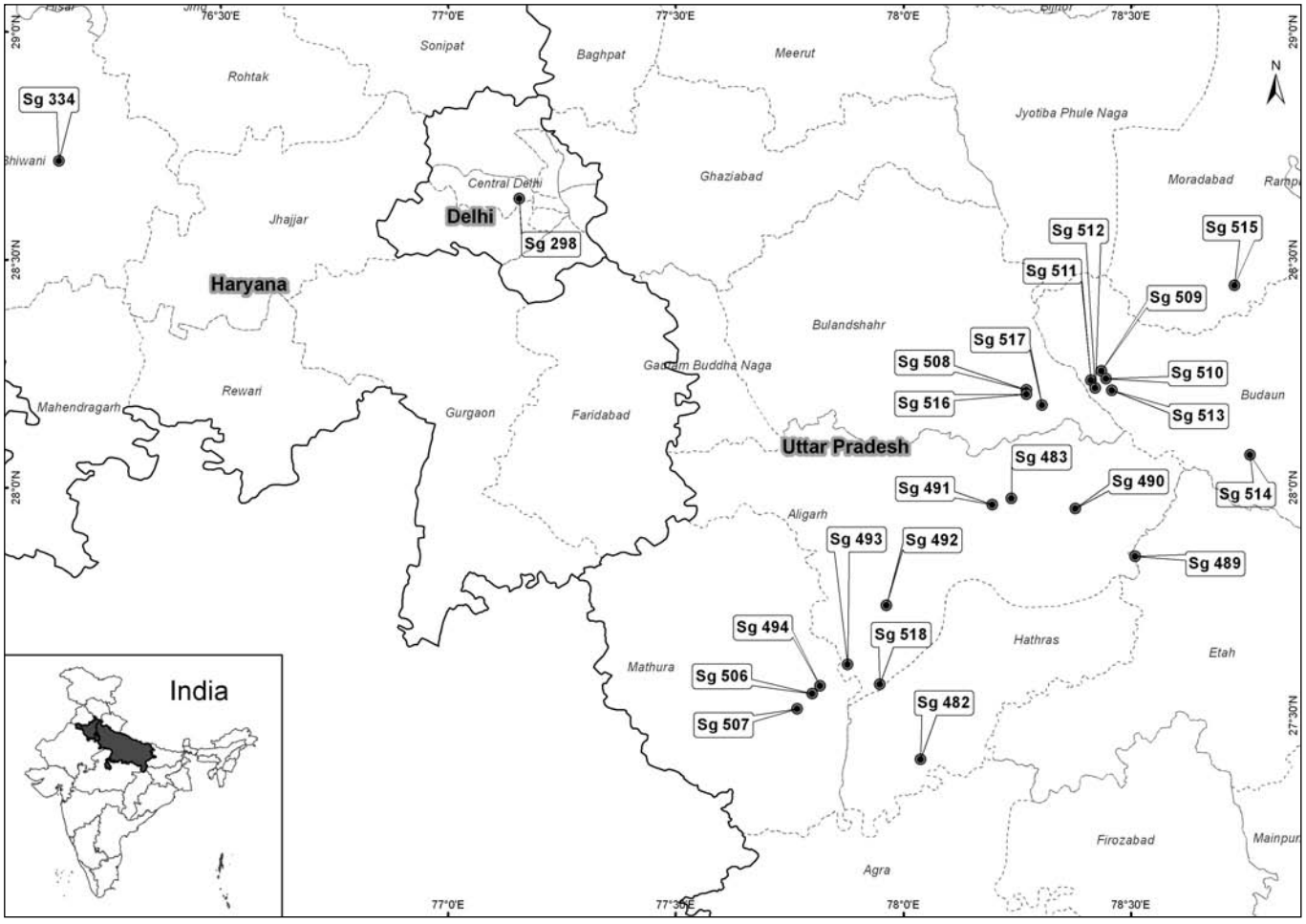

Fig. 1. Origin of *Sclerospora graminicola* isolates collected from Uttar Pradesh (India).

was conducted in a complete randomized design with three replications, and 35-40 seedlings per replication.

Data recording and analysis. Latent period$_{50\%}$ (number of days after inoculation for typical symptom appearance on 50% of the infected seedlings) was recorded from 4th day onwards post inoculation. DM incidence was recorded 14 days post inoculation as percent of infected plants. Quantitative differences in the virulence levels of the isolates were determined by calculating virulence index (percent disease incidence × latent period^{-1}) (Thakur and Rao, 1997).

Data sets were subjected to analysis of variance (ANOVA) to determine significant differences among isolates for latent period, DM incidence and virulence index. Based on the proximity matrix, calculated by using Euclidean distance measure, cluster analysis was done using the Average Linkage method (GENSTAT 9.1, Lawes Agricultural Trust, UK) to determine the similarity among isolates and to classify isolates into different virulence groups based on virulence index.

RESULTS

On farm DM survey. DM was quite severe in all the eight districts of Uttar Pradesh surveyed. A total of 97 fields were surveyed and DM was found in 86 fields (89%) with incidence ranging from 2 to 100% with a mean incidence of 52% across infected fields (Table 2). DM incidence was very high in the Hathras district with 100% incidence. None of the fields surveyed in Badaun, Bulandshehar, Mathura and Moradabad districts were free from DM and the mean DM incidence in these districts ranged from 45 to 83%.

Fifteen hybrid cultivars (Alankar, GK 1044, HS 68, JKBH 26, Kanchan, Kaveri 456, Krishna, Nirmal 1651, PAC 931, SBH 768, Pusa 383, Pioneer 86M32, -86M52, -86M64 and Proagro 9444) were observed on farmers' fields (Table 3). Pioneer 86M32 was observed in 29 of the 97 fields surveyed (36% area surveyed) and DM was quite severe (up to 100% incidence) on this hybrid. Eighteen hybrids of unknown identity were also observed, all of them being susceptible to DM with a range of 44-94% disease incidence. Twenty local cultivars were also observed with relatively low DM inci-

Table 2. Prevalence of downy mildew (DM) in eight Uttar Pradesh districts surveyed during the 2007-08 rainy seasons.

District	Villages (No.)	Fields surveyed		Area (ha) surveyed		DM incidence (%)[a]	
		Total	DM-infected	Total	DM-infected	Mean	Range
Agra	5	21	15	10.0	7.4	28	3-100
Aligarh	13	22	21	14.1	13.7	49	10-93
Badaun	7	19	19	11.8	11.8	49	11-86
Bulandshehar	3	5	5	3.4	3.4	45	12-94
Etah	2	4	3	1.0	0.8	11	2-25
Hathras	2	8	5	3.6	2.4	100	100
Mathura	3	9	9	7.0	7.0	83	61-93
Moradabad	2	9	9	6.0	6.0	51	10-94
Total	37	97	86	56.9	52.5	52	2-100

[a]Based on DM-infected fields.

dence (2 to 29%). Of the 15 hybrids monitored in the field, six (Kanchan, Nirmal 1651, PAC 931, Pioneer 86M52, -86M64 and Proagro 9444) were free from DM, two (Pusa 383 and JKBH 26) were moderately resistant (10-20% incidence) and seven highly susceptible (>50% incidence).

Virulence diversity. Analysis of variance showed significant differences ($P<0.001$) between pathogen isolates, host genotypes and their interactions for DM incidence, latent period and virulence index indicating pathogenic variability among test isolates (Table 4). Percent disease incidence varied from 1 to 100%. Mean DM incidence for the test isolates across differentials ranged from 41% (Sg 508) to 97% (Sg 517) (Table 5). Mean DM incidence in the old isolates Sg 298 (from New Delhi) and Sg 334 (from Bhiwani, Haryana) was 52 and 35%, respectively. Eighteen of the 21 isolates collected from Uttar Pradesh had more than 60% DM incidence across differentials, indicating high levels of virulence in the pathogen populations in farmers' fields. Based on the pathogenicity factor (number of differentials with >10% DM incidence), 23 isolates formed 5 pathogenic groups (Table 6). Group 1, comprising 10 isolates (Sg 483, -489, -490, -492, -493, -494, -507, -511, -513, and -517), was the most virulent and the isolates belonging to this group were virulent on all the seven differentials (pathogenicity factor 7). Group 2, comprising 8 isolates (Sg 491, -509, -510, -512, -514, -515, -516, -518), and isolate Sg 298 from New Delhi was virulent on all differentials except IP 18292 (pathogenicity factor 6). Group 3, represented by Sg 482 was also virulent

Table 3. Prevalence of downy mildew (DM) in different pearl millet cultivars in Uttar Pradesh surveyed during the 2007-08 rainy seasons.

Cultivars	Fields surveyed		Area (ha) surveyed		DM incidence (%)[a]	
	Total	DM-infected	Total	DM-infected	Mean	Range
Alankar	2	2	0.6	0.6	61	60-62
GK 1004	1	1	0.2	0.2	25	-
HS 68	1	1	0.4	0.4	68	-
Unknown hybrids	18	18	12.4	12.4	67	44-94
JKBH 26	5	2	2.3	1.0	11	6-16
Kanchan	1	0	0.2	0.0	0	-
Kaveri 456	4	4	1.6	1.6	54	36-68
Krishna	3	3	2.2	2.2	52	10-93
Local cultivars	20	20	11.3	11.3	13	2-29
Nirmal 1651	1	0	0.4	0.0	0	-
PAC 931	1	0	0.4	0.0	0	-
Pioneer 85M32	29	29	20.7	20.7	52	3-100
Pioneer 86M52	3	0	1.3	0.0	0	-
Pioneer 86M64	1	0	0.4	0.0	0	-
Proagro 9444	1	0	0.4	0.0	0	-
Pusa 383	1	1	0.1	0.1	19	-
SBH 768	5	5	2.0	2.0	51	10-92
Total	97	86 (89%)	56.9	52.5 (92.3%)	28	-

[a]Based on DM-infected fields.

Table 4. Analyses of variance for downy mildew (DM) incidence, latent period and virulence index for 21 *Sclerospora graminicola* isolates collected from Uttar Pradesh.

Source of variation	df	MS		
		DM incidence (%)	Latent period (days)	Virulence index
Replications	2	8.72	3.58	6.02
Isolates (I)	20	7814.81***	38.15***	205.50***
Genotypes (G)	8	21941.79***	58.82***	865.48***
I × G	160	1399.54***	6.23***	40.31***
Residual	376	24.91	0.57	1.72
Total	566			

***Significant at $P<0.001$.

Table 5. Downy mildew incidence of *Sclerospora graminicola* isolates from Uttar Pradesh on pearl millet host differential lines.

Isolate	Downy mildew incidence (%)[a]									
	P 7-4	P 310-17	700651	7042R	852B	IP 18292	IP 18293	ICMP 451	7042S	Mean
Sg 482	23	19	24	39	36	47	10	100	100	44
Sg 483	49	43	62	88	79	21	19	98	100	62
Sg 489	75	81	85	100	97	29	82	96	100	83
Sg 490	73	80	77	67	97	95	45	100	100	82
Sg 491	85	83	90	100	98	10	85	100	100	83
Sg 492	90	70	54	97	99	100	72	100	100	87
Sg 493	91	91	90	94	97	100	68	100	100	92
Sg 494	60	81	43	48	96	100	59	100	100	76
Sg 506	38	25	38	84	0	3	21	100	100	45
Sg 507	100	100	99	69	100	100	100	100	100	96
Sg 508	30	24	45	51	1	5	17	100	100	41
Sg 509	96	100	99	100	100	7	77	100	100	87
Sg 510	100	100	100	100	100	4	73	100	100	86
Sg 511	90	98	63	100	100	14	69	99	100	81
Sg 512	100	90	59	99	100	10	41	99	100	78
Sg 513	91	88	52	66	100	100	51	100	100	83
Sg 514	100	83	46	35	100	3	39	100	100	67
Sg 515	98	83	93	100	100	0	76	99	100	83
Sg 516	100	95	92	100	100	10	91	100	100	88
Sg 517	100	100	98	97	100	100	74	100	99	96
Sg 518	98	100	98	100	100	10	82	99	100	87
Sg 298	29	25	46	54	82	7	26	99	100	52
Sg 334	16	19	17	29	14	10	9	98	100	35
Trial mean	75	73	68	79	82	38	56	99	100	

[a]Mean of 2 runs, 3 replications/entry, 30-35 seedlings/replication.
LSD ($P<0.05$) for isolate means = 1.78; for genotype means = 1.11; for isolate x genotype means = 5.33.

on 6 differentials (pathogenicity factor 6), but avirulent on IP 18293. Isolates Sg 506 and Sg 508 formed group 5 and were the least virulent among the isolates collected from Uttar Pradesh. Bhiwani isolate (Sg 334) represented group 4 and was less virulent (pathogenicity factor 5) and pathogenically different from isolates collected in Uttar Pradesh, whereas the Delhi isolate Sg 298 was similar to 8 of the 21 Uttar Pradesh isolates (pathogenic group 2, Table 6).

A dendrogram generated by the average linkage cluster analysis of virulence index clustered the 23 isolates into 5 major groups (Fig. 2). Based on virulence index, group V appeared as the most virulent group comprising 4 isolates (Sg 490, -492, -493, and -494) with >13 mean virulence index across differentials. Groups II (9 isolates) and III (3 isolates) had moderate to high levels of virulence. Isolate Sg 514 (group IV) with 8.6 virulence index appeared separately in the dendrogram. Isolates

Table 6. Pathogenic groups/pathotypes of *Sclerospora graminicola* isolates based on their reaction on host differentials.

Pathogenic group	Representative isolates	Reaction type[a]							Pathogenicity factor
		700651	7042R	852B	IP18292	IP18293	P310-17	P7-4	
1	Sg 483, -489, -490, -492, -493, -494, -507 -511, -513, -517	+	+	+	+	+	+	+	7
2	Sg 491, -509, -510, -512, -514, -515, -516, -518, -298	+	+	+	–	+	+	+	6
3	Sg 482	+	+	+	+	–	+	+	6
4	Sg 334	+	+	+	–	–	+	+	5
5	Sg 506, -508	+	+	–	–	+	+	+	5

[a]Mean of 3 replications, 35-40 seedlings/replication.
+ = Susceptible (S) (>10% downy mildew incidence); – = Resistant (R) (≤10% downy mildew incidence).

Sg 482, -483, -506 and -508 clustered in the least virulent group I along with old isolates Sg 298 and Sg 334.

DISCUSSION

ICRISAT has a major research focus on development of pearl millet hybrid parent lines, especially diversifying the genetic base of A-lines, which are disseminated to public organizations and private seed companies for use in developing F_1 hybrid cultivars. Breeding lines are screened against different pathotypes in the greenhouse under high disease pressure (>85% disease incidence in the susceptible check) and those found resistant (≤10% disease incidence) to at least two pathotypes are designated and disseminated as seed parents. The isolates collected from Uttar Pradesh were more virulent than the isolates Sg 298 (from New Delhi) and Sg 334 (from Haryana) being used at ICRISAT for greenhouse screening of hybrid parent lines targeted for the north-

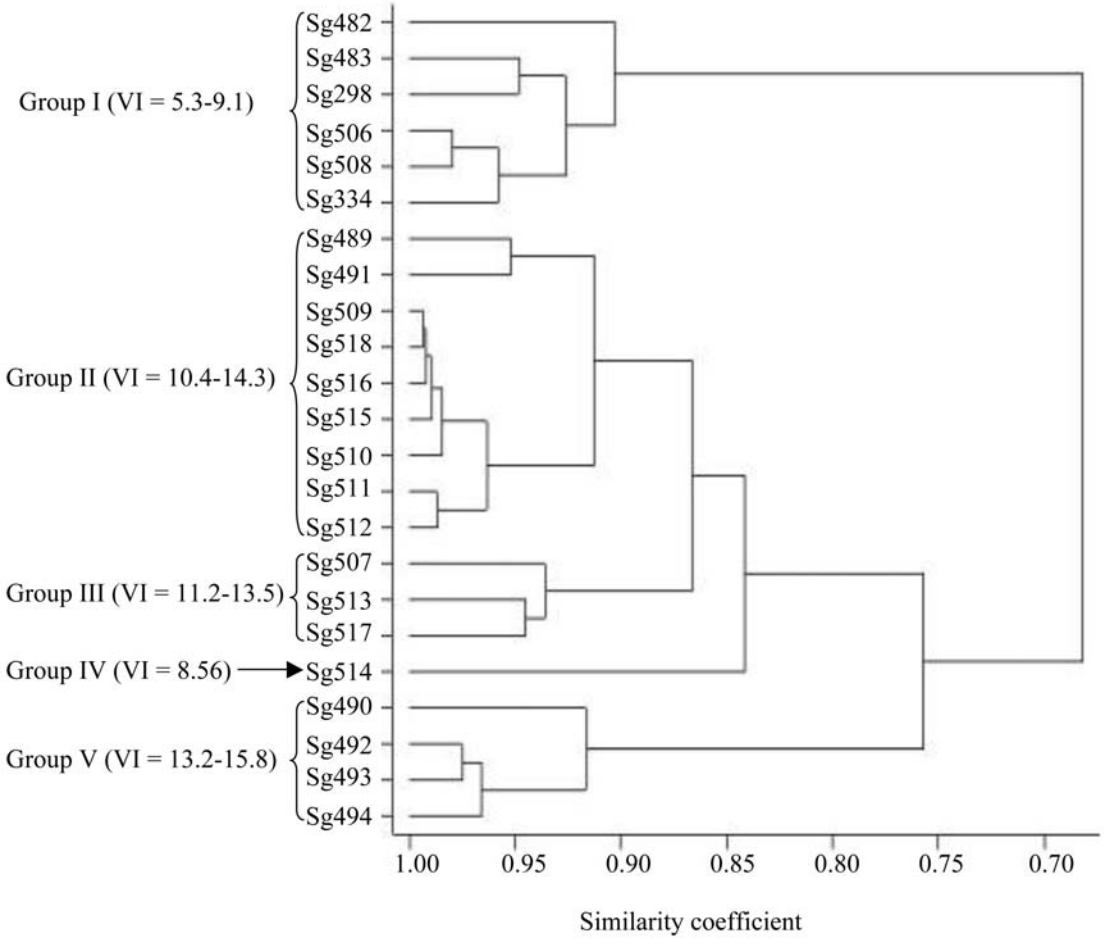

Fig. 2. Grouping of *Sclerospora graminicola* isolates based on virulence index.

ern plains in India. Therefore, these old less virulent pathotypes need to be replaced with new more virulent pathotypes for the greenhouse screening of pearl millet lines targeted for hybrid development for Uttar Pradesh.

In the pearl millet downy mildew pathosystem, disease incidence levels indicate quantitative differences for virulence in the pathogen and resistance in the host. Quantitative variation in *S. graminicola* isolates was studied by calculating the virulence index from two independent measures of pathogenicity, disease incidence and latent period (Thakur and Rao, 1997). Significant differences were observed in the virulence index of the test isolates indicating virulence diversity in isolates from Uttar Pradesh. Differential line IP 18292 recorded minimum mean virulence index (6.4) across 23 isolates tested and <2.5 virulence index against 15 isolates, indicating that resistance in this genotype is comparatively stable and might be governed by several QTLs for downy mildew resistance. The number of QTLs for host plant resistance has been reported in pearl millet against different pathotypes of *S. graminicola* (Hash and Witcombe, 2001; Jones *et al*., 2002).

There was good correspondence between pathogenic and virulence groups. Isolates Sg 490, -492, -493 and -494 from the pathogenic group 1, virulent on all the differentials were clustered in one virulence group (V) with highest virulence index. Similarly, isolates Sg 491, -509, -510, -512, -514, -515, -516, and -518 comprising pathogenic group 2, virulent on 6 differentials were clustered in virulence group II with moderate virulence levels. Isolate Sg 298 (from Delhi) had low virulence index and was grouped in less virulent group I along with other less virulent isolates Sg 334 (from Bhiwani). The overlap between pathogenic and virulence groups may be due to the same genes for pathogenicity and virulence, however, in addition to major genes for pathogenicity, some minor genes may be responsible for quantitative differences in the virulence of these isolates.

The main objective of this study was to characterize pathogen populations from Uttar Pradesh state and to select highly virulent and geographically diverse isolates for greenhouse screening of pearl millet lines targeted for this Indian region. This is the first report on pathogenic diversity study in the *S. graminicola* populations from the northern Indian plains. From this study, we could select two highly virulent isolates Sg 492 from Aligarh and Sg 510 from Badaun two locations more than 100 km apart. Thus, these two isolates from Uttar Pradesh in addition to one each from New Delhi and Bhiwani will be used for greenhouse screening of pearl millet breeding lines targeted for hybrid development best suited for northern India.

ACKNOWLEDGEMENTS

The authors like to thank Dr I.S. Khairwal, Project Coordinator, All India Coordinated Pearl Millet Improvement Project, for approving and Dr R.S. Mahala, Pioneer Overseas Corporation, Hyderabad, for facilitating the on-farm survey.

REFERENCES

Hash C.T., Witcombe J.R., 2001. Pearl millet molecular marker research. *International Sorghum and Millet Newsletter* **42**: 8-15.

Idris M.O., Ball S.L., 1984. Inter- and intracontinental sexual compatibility in *Sclerospora graminicola. Plant Pathology* **33:** 219-223.

Jeger M.J., Gilijamse E., Bock C.H., Frinking H.D., 1998. The epidemiology, variability and control of the downy mildews of pearl millet and sorghum, with particular reference to Africa. *Plant Pathology* **47**: 544-569.

Jones E.S., Breese W.A., Liu C.J., Singh S.D., Shaw D.S., Witcombe J.R., 2002. Mapping quantitative trait loci for resistance to downy mildew in pearl millet: field and glasshouse screens detect the same QTL. *Crop Science* **42**: 1316-1323.

Kolmer J.A., Long D.L., Hughes M.E., 2006. Physiologic specialization of *Puccinia triticina* on wheat in the Unites States in 2004. *Plant Disease* **90**: 1219-1224.

Michelmore R.W., Pawar M.N., Williams R.J., 1982. Heterothallism in *Sclerospora graminicola*. *Phytopathology* **72**: 1368-1372.

Pushpavathi B., Thakur R.P., Chandrashekara Rao K., 2006a. Fertility and mating type frequency in Indian isolates of *Sclerospora graminicola*, the downy mildew pathogen of pearl millet. *Plant Disease* **90**: 211-214.

Pushpavathi B., Thakur R.P., Chandrashekara Rao K., Rao V.P., 2006b. Characterization of *Sclerospora graminicola* isolates from pearl millet for virulence and genetic diversity. *Plant Pathology Journal* **22**: 28-35.

Rao V.P., Thakur R.P., Rai K.N., Sharma Y.K., 2005. Downy mildew incidence on pearl millet cultivars and pathogenic variability among isolates of *Sclerospora graminicola* in Rajasthan. *International Sorghum and Millets Newsletter* **46**: 107-110.

Sastry J.G., Sivaramakrishnan S., Rao V.P., Thakur R.P., Singru R.S., Gupta V.S., Ranjekar P.K., 2001. Genetic basis of host specificity in *Sclerospora graminicola*, the pearl millet downy mildew pathogen. *Indian Phytopathology* **54**: 323-328.

Sharma R., Rao V.P., Varshney R.K., Prasanth V.P., Kannan S., Thakur R.P., 2010. Characterization of pathogenic and molecular diversity in *Sclerospora graminicola*, the causal agent of pearl millet downy mildew. *Archives of Phytopathology and Plant Protection* **43**: 538-551.

Sivaramakrishnan S., Thakur R.P., Kannan S., Rao V.P., 2003. Pathogenic and genetic diversity among Indian isolates of *Sclerospora graminicola* from pearl millet. *Indian Phytopathology* **56**: 392-397.

Thakur R.P., Shetty K.G., King S.B., 1992. Selection for host-specific virulence in asexual populations of *Sclerospora graminicola*. *Plant Pathology* **41**: 626-632.

Thakur R.P., Rao V.P., 1997. Variation in virulence and aggressiveness among pathotypes of *Sclerospora graminicola* on pearl millet. *Indian Phytopathology* **50**: 41-47.

Thakur R.P., Rao V.P., Amruthesh K.N., Shetty H.S., Datar V.V., 2003. Field surveys of pearl millet downy mildew- effects of hybrids, fungicide and cropping sequence. *Journal of Mycology and Plant Pathology* **33**: 387-394.

Thakur R.P., Rao V.P., Wu B.M., Subbarao K.V., Shetty H.S., Singh G., Lukose C., Panwar M.S., Sereme Paco Hess D.E., Gupta S.C., Dattar V.V., Panicker S., Pawar N.B., Bhangale G.T., Panchbhai S.D., 2004. Host resistance stability to downy mildew in pearl millet and pathogenic variability in *Sclerospora graminicola. Crop Protection* **23**: 901-908.

Thakur R.P., Shetty H.S., Khairwal I.S., 2006. Pearl millet downy mildew research in India: progress and perspectives. *International Sorghum and Millets Newsletter* **47**: 125-130.

Williams R.J., 1984. Downy mildew of tropical cereals. *Advances in Plant Pathology* **3**: 1-103.

Received May 20, 2010
Accepted August 10, 2010