RECOVERY RESISTANCE TO DOWNY MILDEW IN PEARL MILLET PARENTAL LINES ICMA 1 AND ICMB 1

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Abstract

Downy mildew [Sclerospora graminicola (Sacc.) Schroet.] has been a major biotic factor affecting grain yield of pearl millet [Pennisetum glaucum (L.) R.Br.] in India for the last 25 yr. Many downy mildew resistant cultivars have been produced and several have been cultivated widely, but the vulnerability of their resistances to the disease has been a major cause of concern. Recovery resistance, in which the pathogen completes its life cycle without affecting the normal development of the plant, has potential for providing durable resistance to the disease. A high level of recovery resistance (\geq 95%) was developed in ICMA 1 (81A, a leading male-sterile line in India) and its maintainer line ICMB 1 (81B), through pedigree selection for five generations. The recovery trait in the selected line, designated as RECRES 81A, was stable against the major pathotypes present in India. RECRES 81A is agronomically and phenotypically similar to 81A, produces equally high yielding hybrids, and is being used to produce commercial hybrids.

D^{OWNY MILDEW} is the major biotic constraint to the full exploitation of high grain yield potential of improved cultivars, particularly F_1 hybrids, of pearl millet in India (Safeeulla, 1977; Singh et al., 1987). During the last 25 yr, severe epiphytotics of the disease have caused substantial yield losses, resulting in the withdrawal from cultivation of several otherwise novel genotypes (Singh et al., 1993). Control of the disease by use of fungicides (Singh and Shetty, 1990) and by conventional host plant-resistance, in which a cultivar may possess both resistant and susceptible plants, has been successful (Singh et al., 1987; Talukdar et al., 1994). However, the disease has remained a serious cause of concern because of the vulnerability of resistances deployed in single cross hybrids (Singh, 1994).

Singh and King (1988) reported a new type of resistance to the disease, *recovery resistance*, in which a plant may develop the systemic disease symptoms but subsequently outgrow the disease within a week of infection. This is a unique host-pathogen relationship in which the host allows the pathogen to complete its life cycle, and the latter in turn, does not affect normal growth and grain yield of the host. This phenomenon has also been discovered with downy mildews of sorghum [Sorghum

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bicolor (L.) Moench] (Singh and de Milliano, 1989) and maize (Zea mays L.) (Olanya and Fajemisin, 1992).

Preliminary screening results have shown that 80% of pearl millet accessions from several west African countries possessed 10 to 80% plants showing recovery resistance (S.D. Singh, 1988, Studies on recovery resistance to downy mildew in pearl millet. p. 276. Unpublished abstracts of the Int. Congress of Plant Pathology, 5th, Kyoto, Japan. 20–27 Aug. 1988). Recovery resistance is dominant over both conventional resistance and susceptibility. Occurrence of recovery also has been observed in breeding lines developed at ICRISAT Center, (S.D. Singh, 1989, unpublished data).

Based on this information, selection was practiced for recovery resistance in ICMA 1 and ICMB 1, which are commonly known as 81A and 81B, (Anand Kumar et al., 1984), with the objective of achieving increased expression of recovery resistance in a genetic background suitable for direct commercial exploitation.

Materials and Methods

Approximately 20 seed of ICMA 1 (downy mildew resistant selection of Tift 23 DB developed by irradiation, Anand Kumar et al., 1984) and ICMB 1 (maintainer line of ICMA 1) were sown in each of ten 20-cm-plastic pots filled with Alfisol (clayey-skeletal mixed isohyperthermic Udic Rhodustalfs) and farm vard manure (3:1; v/v). Seedlings were spray-inoculated at the coleoptile-to-first leaf stage with a sporangial suspension $(1 \times 10^6 \text{ sporangia mL}^{-1})$ of Patancheru (India) pathotype. Inoculation was conducted in an inoculation chamber maintained at 20 \pm 2°C and >95% relative humidity (RH) in the dark and the pots were retained under these conditions for 16 hr to establish infection. The pots were then transferred to greenhouse benches where the air temperature was maintained at 25 \pm 2°C. Observations on disease incidence were made 2 wk after inoculation (Singh and Gopinath, 1985). The diseased plants that recovered were tagged and percent recovery was determined.

At flowering, all downy mildew-recovered (S₀) plants of ICMB 1 were selfed and simultaneously crossed to recovered (S_0) plants of ICMA1. Selfed progenies of ICMB 1 (S_1) and the crossed progenies of ICMA 1 (ICMA 1 \times ICMB 1) (F₁) were grown in the field disease nursery (Singh et al., 1993) up to four generations (1983-1987), and the process of selection, selfing, and crossing of recovered plants was repeated during each generation. Plants that recovered but exhibited stunted or slow growth were discarded. The progeny, referred to hereafter as RECRES 81A, was tested for the recovery reaction at three downy mildew-infested locations (Patancheru, Mysore, Aurangabad) in India during 1991. The trial was conducted in a randomized complete block design with two replications. The plot size was two rows, 4 m long. The line was also tested against four pathotypes (Patancheru, Mysore, Aurangabad, Rajasthan) under greenhouse conditions at ICRISAT Center, following a completely randomized block design with two replications. There were five pots in each replication. These four major pathotypes of S. graminicola in India are routinely

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Table 1. Selection and advance of progenies of ICMB 1, mean downy mildew (DM) incidence (%), and mean recovery (%), from S_0 (greenhouse) to S_4 in field DM nurseries at ICRISAT Asia Center, Patancheru during 1983 to 1987.

	Generations									
Entry	S ₀ †	Sı	SE	S_2	SE	S3	SE	S4	SE	
ICMB1										
No. of progenies	181	8	_	10	_	16	-	4	-	
Mean DM incidence (%)	16	52	±2.3	58	±3.7	76	± 5	93	± 1.75	
Mean recovery (%) NHB3 (Susc. control)	27	60	±4.8	74	± 3.7	84	±2.5	95	±1	
(% DM incidence)	88	72		79		92		91		

 \dagger Figures under S_0 are total plants, percent downy mildew incidence, and percent recovery, respectively.

used in evaluation of breeding materials at ICRISAT Center (S.D. Singh, 1990, unpublished data).

 F_1 hybrids produced on 81A and RECRES 81A using a common pollinator, BSEC TCP2, were compared for plant height, days to 50% bloom, panicle length, and grain yield in a trial at Patancheru (17°20'N) and Gwalior (26°14'N) during the 1991 rainy season. Each entry was sown in four rows, 4 m long, with three replications arranged in a randomized block design. The experiment was conducted in Alfisol under high fertility conditions (80 kg N, 40 kg P₂O₅ ha⁻¹). Grain yield data was recorded from the two center rows only. Data on time to 50% bloom were recorded on whole plot basis and on plant height and panicle length on the basis of five random plants. Statistical analysis was done according to Cochran and Cox (1957).

Results and Discussion

Twenty-seven percent of the systemically infected plants of ICMB1 that developed systemic infection following artificial inoculation recovered under greenhouse conditions (Table 1). Head-to-row progenies from eight selected plants showed increased levels of recovery in the S_1 generation. Further selection and advancement under disease nursery conditions resulted in the progressive increase of lines with recovery resistance, reaching a mean of 95% in the S_4 generation. As expected, 100% recovery was not found in the S₁ or subsequent generations. This may be due either to escapes in the disease nursery or to a few plants in the selected progenies that were segregating for this character and that were providing a certain degree of residual variability (Singh et al., 1992). It may also be due to an extremely small manifestation of the disease on one or several of the basal leaves, followed by recovery so rapid that these plants would not have been counted as infected and

Table 2. Reaction of RECRES 81A to downy mildew at three highly infested locations, and to four pathotypes from India under greenhouse conditions during 1991 at ICRISAT Asia Center (IAC).

Pathotype Mysore			Control [†]		
	Environment	No. total plants	No. diseased plants	Recovery‡ (%)	Downy mildew incidence (%)
	Mysore field	180	157	94	90
	Greenhouse, IC	205	180	98	95
Patancheru	Patancheru field	231	200	90	96
Greenhouse, I	Greenhouse, IC	187	177	95	98
Aurangabad	Aurangabad field	130	60	97	68
U	Greenhouse, IC	209	190	98	93
Rajasthan	Greenhouse, IC	190	182	98	83

† Downy mildew susceptible cultivar HB 3 was used as control.

\$\$\propto the covery is based on the total number of diseased plants and plants that recovered from the disease.

subsequently were not included in plants evaluated for recovery resistance.

RECRES 81A also showed high levels of recovery (90–97%) in the disease nursery at three heavily-infested locations (Patancheru, Mysore, and Aurangabad) in India and also against the four pathotypes of the pathogen under greenhouse conditions (95–98%) at ICRISAT Center (Table 2). Thus, the recovery resistance trait was stable in expression across these locations and pathotypes in India.

The F_1 hybrids produced on 81A and RECRES 81A were statistically similar for days to 50% bloom, plant height, panicle length, and grain yield (Table 3), indicating that pedigree selection for recovery resistance had no effect on specific combining ability of the line. RECRES 81A is currently being used for production of commercial hybrids in India.

The strategic significance of recovery resistance is two fold. First, cultivars with recovery resistance develop disease depending on disease pressure and environment, but subsequently recover and express no symptoms when compared with cultivars with conventional resistance. Since the plants express the disease for a very short period, growth, grain yield, and combining ability of the recovered plants remain unaffected. Secondly, the pathogen completes its life cycle on all infected plants (Singh, 1995), so that selection pressure for virulence is either absent or perhaps less than when conventional resistance is deployed. These factors may contribute to a durable resistance mechanism in commercial cultivars. Further studies on the mechanism of this type of resis-

Table 3. Grain yield and three other agronomic traits in hybrids based on 81A and RECRES 81A at two field locations in India during 1991.

Entry	Grain yield (kg ha ⁻¹)			Time to 50% bloom (d)			Plant height (cm)			Panicle length (cm)		
	PHF†	GHF‡	Mean	PHF	GHF	Mean	PHF	GHF	Mean	PHF	GHF	Mean
RECRES 81A × BSEC TCP2 (Rec.)	3610	3070	3340	46	47	47	176	242	209	22	28	25
81A × BSEC TCP2§	3670	2970	3320	44	47	46	159	238	198	21	29	25
Trial mean	3350	3180	3270	42	45	43	149	219	184	19	25	22
SE+	231	277	180	0.8	1.6	0.9	17	8	10	2.4	1.8	1.5
CV(%)	12	15	-	3	6	-	20	7	-	22	13	-

† PHF = Patancheru High Fertility.

‡ GHF = Gwalior High Fertility.

§ BSEC TCP2 = Bold [1000 seed mass > 10g] Seeded Early Composite Topcross Pollinator 2.

tance, its inheritance, and its durability under field conditions are in progress.

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NATURAL OUTCROSSING IN CHICKPEA (CICER ARIETINUM L.)

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Abstract

The rate of natural outcrossing in the cultivated chickpea (Cicer arietinum L.) was estimated with five lines grown over three planting dates in the 1988-1989 season, and four other lines grown in one planting date in 1989, and over two planting dates in 1991. At each planting date, a randomized complete block design with six replications was employed. The location of the study was at the University of California, South Coast Research and Extension Center, Irvine, CA, where high outcrossing rates have been previously observed in different genotypes of the common bean (Phaseolus vulgaris L.). Compound leaf, controlled by a single dominant gene (Silv/silv), was used as a morphological marker. Unifoliate genotypes were used as female parents and were interplanted in the middle row of every plot with genotypes with compound leaves designated as male parents. Although many bumble bees (Bombus spp.) and honey bees (Apis mellifera L.) visited open chickpea flowers, progeny tests revealed that the average rate of natural outcrossing in the lines under investigation was less than 1%.

CHICKPEA or garbanzo is characterized by cleistogamous flowers and is presumed to be a completely self-pollinating species, and it is treated as such by plant breeders (Auckland and van der Maesen, 1980; Singh, 1987; Muehlbauer et al., 1988). However, there are indications that a small amount of natural cross-

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of sorghum from downy mildew in Zimbabwe. Plant Dis. 73: 1020.

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pollination by bees may occur under field conditions. Reports from India, Israel, and Syria revealed that the rates of natural outcrossing in the crop range from 0 to 2% (Howard et al., 1915; Eshel, 1968; Niknejad and Khosh-khui, 1972; Gowda, 1981; Malhotra and Singh, 1986; van der Maesen, 1987). A thorough knowledge of the mode of pollination of a species under a particular environment plays a crucial role in planning breeding and selection programs for successful improvement of the crop. In most self-pollinating species, the level of outcrossing is so low that no protective measures are required during line purification and seed increase; whereas, in some other cases, as in sesame (Sesamum indicum L.), protection might be required to assure complete self-pollination (Briggs and Knowles, 1967). A low level of outcrossing permits new gene combinations and might be beneficial in introducing variation into the breeding populations. This would be desirable in chickpea since production of hybrids by hand-pollination is tedious and time consuming. The percentage of successful hand pollinations ranges between 0 to 50% and depends both on the individual performing the crosses and the environment (Bahl and Gowda, 1975; Bahl, 1988; Tayyar, 1990, unpublished results). Moreover, seemingly successful hand-pollinations often abort the developing pods under both glasshouse and field conditions. Recently, Wells et al. (1988) reported unusually high outcrossing rates in the common bean (Phaseolus vulgaris L.), a self-pollinating species (Allard, 1960), when tested at the University of California South Coast Research and Extension Center, Irvine, CA. These rates ranged from 0 to 66.8% with an average value of 28.5%. which is considerably higher than any previously cited rate for common beans from either a temperate or tropical area. A similar range of outcrossing rate (0-78%), but

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