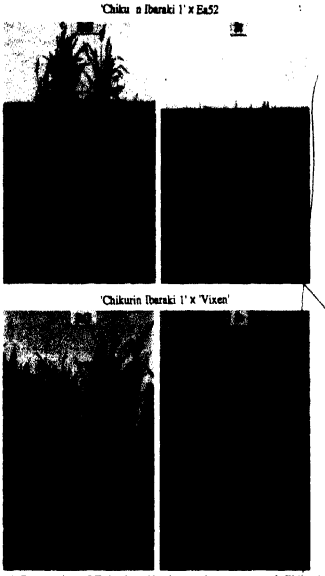

Fig. 4: Segregation of F_2 barley (*Hordeum vulgare*) plants of 'Chikurin Ibaraki 1' × Ea52 and 'Chikurin Ibaraki 1' × 'Vixen' in field conditions to isolates RG and 2t of the BYDV-PAV

whereas Ea52 was resistant and a resistance gene in Ea52 (*ym3*) was identified (Ukai and Yamashita 1987). 'Chikurin Ibaraki 1' was resistant to BaMMV whereas its mutant Ea52 was susceptible (Götz et al. 1991) and the resistance in 'Chikurin Ibaraki 1' to BaMMV was shown to be conditioned by a single recessive gene (Ordon and Friedt 1993). It would be of interest to investigate the genetic relationships between the genes conferring resistance to the three different viruses (BYDV-PAV, BaYMV and BaMMV).

References

Baltenberger, D. E., H. W. Ohm, and J. E. Foster, 1987: Reactions of oat, barley and wheat to infection with barley yellow dwarf virus. Crop Sci. **27**, 195–198.

Catherall, P. L., A. T. Jones, and J. D. Hayes, 1970: Inheritance and effectiveness of genes in barley that condition tolerance to barley yellow dwarf virus. Ann. Appl. Biol. **65**, 153–161.

Chalhoub, B. A., A. Sarrafi, M. A. Beuve, and H. D. Lapierre, 1994: Differential interaction between PAV-like isolates of barley yellow dwarf virus and barley (*Hordeum vulgare* L.) genotypes. J. Phytopathology **142**, 189–198.

Conti, M., C. J. D'arcy, H. Jedlinski, and P. A. Burnett, 1990: The 'yellow plague' of cereals, barley yellow dwarf virus. In: P. A. Burnett (ed.), World Perspectives on Barley Yellow Dwarf, 1–6. CIMMYT, Mexico City.

Damsteegt, V. D., and G. W. Bruehl, 1964: Inheritance of resistance in barley to barley yellow dwarf. Phytopathology **54**, 219–224.

Götz, R., F. Ordon, and W. Friedt, 1991: Resistance to the 'barley yellow mosaic virus complex' and genetic diversity of BaMMV-resistance. Barley Genetics VI, Proc. 6th Int. Barley Genet. Symp. Helsingborg, Sweden, 610–614.

Jones, A. T., and P. L. Catherall, 1970: The relationship between growth rate and the expression of tolerance to barley yellow dwarf virus in barley. Ann. Appl. Biol. **65**, 137–145.

Ordon, F., and W. Friedt, 1993: Mode of inheritance and genetic diversity of BaMMV resistance of exotic barley germplasms carrying genes different from '*rm4*'. Theor. Appl. Genet. **86**, 229–233.

Parry, A. L., and R. M. Habgood, 1986: Field assessment of the effectiveness of a barley yellow dwarf virus resistance gene following its transference from spring to winter barley. Ann. App. Biol. **108**, 395–401.

Rasmusson, D. C., and C. W. Schuller, 1959: The inheritance of resistance in barley to the yellow-dwarf virus. Agronomy J. **51**, 661–664.

Rochow, W. F., and L. E. Carmichael, 1979: Specificity among barley yellow dwarf viruses in enzyme immunosorbent assays. Virology **95**, 415–420.

Schaller, C. W., C. O. Qualset, and J. N. Rutger, 1964: Inheritance and linkage of the *Yd2* gene conditioning resistance to barley yellow dwarf disease in barley. Crop Sci. **4**, 544–548.

Skaria, M., R. M. Lister, J. E. Foster, and G. Shaner, 1985: Virus content as an index of symptomatic resistance to barley yellow dwarf virus in cereals. Phytopathology **75**, 212–216.

Suneson, C. A., 1955: Breeding for resistance to barley yellow dwarf virus in barley. Agronomy J. **47**, 283.

Ukai, Y., and A. Yamashita, 1987: Induced mutants highly resistant to barley yellow mosaic virus. In: Barley Genetics V, Proc. 5th. Int. Barley Genet. Symp. Okayama, Japan, 279–286.

Waterhouse, P. M., F. E. Gildow, and G. R. Johnstone, 1988: Luteovirus group. Commonw. Mycol. Inst. Assoc. Appl. Biol. Description of Plant Viruses No. 339. Kew.

Plant Breeding 114, 308—312 (1995)

ISSN 0179-9541

Recurrent selection for downy-mildew resistance in pearl millet

E. Weltzien R.[1] and S. B. King[2]

[1] International Crops Research Institute for the Semi-arid Tropics (ICRISAT), Patancheru 502 324, Andhra Pradesh, India; [2] EARCAL/ICRISAT, P.O. Box 39063, Nairobi, Kenya

With 1 figure and 4 tables

Received March 15, 1994/Accepted January 9, 1995
Communicated by H. H. Geiger

Abstract

One population of pearl millet (*Pennisetum glaucum* (L.) R. Br.) highly susceptible to downy mildew (*Sclerospora graminicola* (Sacc.) Schroet.) was subjected to two cycles of recurrent selection for downy mildew resistance using a modified greenhouse screening method. The response to selection was evaluated under greenhouse and field conditions using 50 random S_1 progenies and 50 random full-sib progenies from each cycle bulk. Significant progress over cycles of selection was observed in all evaluation trials. These results demonstrated that, in a susceptible population, recurrent selection effectively increased the level of resistance to downy mildew. The modified greenhouse method for assessing resistance to downy mildew effectively differentiated genotypes and had the advantages of greater rapidity and suitability for use throughout the year, independent of season.

A rapid decline of genotypic variance was observed in advanced cycles of selection, indicating that a small number of genes controls downy-mildew resistance in this population. The comparison of genotypic and error variance components from S_1 progenies and full-sib progenies suggested that full-sib progenies can be used successfully in recurrent selection for increased downy-mildew resistance.

Key words: *Pennisetum glaucum* — *Sclerospora graminicola* — downy mildew resistance — germplasm utilization — recurrent selection

Pearl millet (*Pennisetum glaucum* (L.) R. Br.) is a short-season cereal crop generally grown in the dry areas of the tropics on sandy and degraded soils. It is the staple food of the semi-arid and arid areas in Africa and in northwestern India, where landrace varieties are predominantly grown because of their adaptation to heat and drought. However, the landrace material from northwestern India is highly susceptible to downy mildew caused by *Sclerospora graminicola* (Sacc.) Schroet (Bidinger et al. 1994). Direct use of this material in breeding new cultivars adapted to the edaphic and climatic conditions of this region will depend on the possibility of improving its resistance to this disease.

During a typical growth cycle, oospores of the pearl millet downy mildew pathogen, which can survive for many years in the soil, infect seedlings of pearl millet. After infection of the meristematic tissue, the mycelium spreads systemically throughout the plant, and sporangiophores with sporangia are formed on leaf surfaces. Sporangia become airborne and upon contact with free water, such as dew or rain droplets on a leaf surface, they liberate zoospores (asexual spores). The infection with zoospores can result in systemic infection if the growing point is invaded. New oospores are produced sexually by compatible mating types (Michelmore et al. 1982).

Thus, under suitable environmental conditions, the disease can spread rapidly to nearby plants and nearby fields, especially during the early stages of plant growth (Michelmore et al. 1982, Shetty 1987, Pinard 1989). Seedling symptoms range from partial discolouration to seedling death. Plants show stunted growth, yellowing, and sometimes 'green ears' (vegetative proliferation of floral parts), which result in partial or complete loss of seed formation in the panicles (Williams 1984).

The field screening procedure is time-consuming as normally a whole crop cycle is used for this test. The success of the screening is highly dependent on weather conditions that favour disease development, and, thus, large differences in disease levels can occur over seasons. A greenhouse screening procedure (ICRISAT 1988) that involves testing of seedlings reduces the time required for screening to about 3 weeks. The procedure is largely independent of season and can thus be easily used as an initial stage of selection in diverse recurrent selection schemes.

The first objective of this study was to investigate the feasibility of improving resistance to downy mildew in the highly susceptible landrace material from northwestern India. The second objective was to determine whether recurrent selection for downy-mildew resistance under greenhouse screening conditions leads to increased resistance in the seedling (greenhouse and field) and adult plant (field). A third objective was to study the effect of two cycles of selection for resistance in the greenhouse on the genetic variability for resistance under greenhouse and field conditions.

Materials and Methods

Genetic materials: The Western Rajasthan Population (WRajPop 88) was established in 1988 by randomly mating 13 landrace accessions of pearl millet from northwestern India. Two random matings with moderate mass selection for seed set, earliness and tillering were done at ICRISAT Center during the rainy season of 1988 and the dry season of 1989. During the 1989 rainy season, 330 single plants were selfed at Fatehpur and Jodhpur in northwestern India, in the state of Rajasthan. The selection experiment was initiated with these 330 S_1 progenies. The recurrent selection procedures which followed are summarized in Table 1. To make full-sib progenies (FSP) among S_1 progenies (S_1P) bulk pollen from single S_1P was used to pollinate 3–4 plants in the other parental S_1P. Crosses among the S_1P were made as a partial diallel to avoid assortative mating for traits such as maturity. To constitute the improved cycle bulks, equal quantities of seed from each cross were bulked. Experiments evaluating the response to selection were conducted with 50 random S_1P and 50 random FSP from each of the C_0, C_1 and C_2 cycle bulks. These S_1P and FSP were all produced during the post-rainy season of 1990 at the ICRISAT Center.

In the evaluation experiments, the inbred lines ICMP 423 (highly

 0179–9541/95/1404–0308 $ 11.00/0

Table 1: Procedure for two cycles of recurrent selection for downy-mildew resistance in WRajPop 88

Year	Season	Activity
1989	Rainy season	330 single plants from C_0 self-pollinated in Rajasthan
1989	Post-rainy season	330 S_1 progenies screened in a greenhouse for downy-mildew resistance
1990	Summer season	40 selected S_1 progenies recombined by making full-sib progenies to form C_1 cycle (12% selection intensity) 245 full-sib progenies screened in a greenhouse for downy-mildew resistance
1990	Rainy season	42 selected full-sib progenies recombined to form C_2 cycle (17% selection intensity)
1990	Post-rainy season	Random full-sib progenies and random S_1 progenies from the C_0, C_1, C_2 cycle bulks produced

resistant), 81B (moderately resistant) and 843B (susceptible) were included five times per replication as control entries. The open-pollinated bulk of NHB3 (a highly susceptible hybrid) and 7042 (a highly susceptible landrace from Chad) was included four times per replication as a control entry.

Greenhouse screening for downy-mildew resistance: The greenhouse screening procedure for downy-mildew resistance was a modification of that reported by Singh and Gopinath (1985). Instead of inoculating plants individually, they were inoculated en masse. Fifty seeds were sown per 10 cm pot, with two pots per entry and a uniform sowing depth of 1 cm, using a potting mixture of sand and soil of 1:1. This generally resulted in >45 plants per pot. At the coleoptile to one-leaf stage, plants were spray-inoculated with an aqueous suspension of sporangia (about 10^5 sporangia ml). Inoculated plants were incubated overnight at 20 °C and >95% RH. Pots were returned to greenhouse benches and the number of plants with systemic mildew symptoms was counted about 2 weeks later. This procedure was used for the selection experiments and for the greenhouse evaluation of progress from selection. The S_1P and FSP for evaluating progress from selection were tested at the same time during the rainy seasons of 1991 in two separate simple 13 × 13 lattice trials.

Field screening for downy-mildew resistance: Spreader rows of the highly susceptible bulk of NHB3 and 7042 were sown every 9th row, as described by Williams et al. (1981). The test entries were sown when more then 75% plants in spreader rows were infected and sporulating abundantly. Plots were single rows of 2 m length, spaced 60 cm apart. The entries were randomized according to a simple 13 × 13 lattice design. Plots were oversown and thinned to about 20 plants per row, 14 days after sowing. The total number of plants and plants with downy-mildew symptoms were counted 30 days after sowing. Plants with downy-mildew symptoms were removed from the plots at the time of the first count. The number of plants with downy-mildew symptoms was again counted at flowering. The trial was conducted in the post-rainy season of 1991.

Statistical analysis: The downy-mildew incidence data (% infected plants) from the evaluation trials were transformed to square roots to achieve normal distribution for analysis of variance. Duncan's multiple-range test was performed on the transformed means to test the significance of differences (Steel and Torrie 1980). The means are presented as percentage incidence (retransformed), whereas variances and components of variance are reported from transformed data. As the lattice design did not increase efficiency, the data were analysed according to a randomized complete-block design, using the ANOVA and VARCOMP procedures of SAS (SAS 1991).

Results

Direct responses to selection

Significant increases in resistance to downy mildew through recurrent selection were apparent (Table 2) in both the S_1P and FSP evaluated in the greenhouse. The initial cycle bulk (C_0) had S_1P and FSP mean levels of resistance similar to the susceptible inbred control, 843B, whereas the second cycle bulk (C_2) means reached levels of resistance that were not significantly different from the resistant controls, ICMP 423 and 81B. The first improved cycle bulk (C_1) showed levels of resistance that were intermediate between the C_0 and the C_2 means for both S_1P and FSP. The same trends were observed for seedling resistance in the field evaluations, except that, for S_1P evaluation, the differences between consecutive cycle means were not significant.

Genotypic variance for downy-mildew resistance at the seedling stage decreased rapidly over selection cycles (Table 3). After the second cycle of improvement, the residual genetic variation was too small to expect further significant gains for resistance, especially when estimated from S_1P performance. The error variances also tended to decrease, possibly due to scale effects, but not nearly as much as the genotypic variances. The same variance components for an unrelated trait, panicle length, showed no decrease of genetic variation. The genotypic variance tended to be larger among the FSP than among the S_1P for seedling resistance in the greenhouse (except for the C_1), as well

Table 2: Progress from one cycle of S_1 progeny (S_1P) selection and a subsequent cycle of full-sib progeny (FSP) selection for seedling downy-mildew resistance (% infected plants) in the WRajPop 88 population of pearl millet

	Greenhouse evaluation		Field evaluation	
	S_1P	FSP	S_1P	FSI
Cycle				
C_0	10.2 c	15.6 c	4.3 d	13.4 c
C_1	5.2 b	4.9 b	3.4 cd	3.8 b
C_2	2.1 a	3.0 a	1.6 abc	1.8 a
Controls				
ICMP 423	2.7 abc	2.4 a	0.0 a	0.8 a
81B	4.2 abc	2.3 a	0.9 ab	1.9 ab
843B	8.7 abc	32.7 d	3.3 bcd	9.9 c
NHB3/7042	34.5 d	57.7 e	42.7 e	64.8 d

a–e: Means within columns that are followed by different letters are significantly different at P = 0.05

Table 3: Estimates of genotypic (s^2_g) and error (s^2_e) variances among 50 random S_1 progenies (S_1P) and full-sib progenies (FSP) derived from the initial and the two improved population bulks of WRajPop 88 after selection for downy-mildew resistance in the greenhouse

Character/ progeny type	Variance component	Cycle of selection C_0	C_1	C_2
Downy mildew, greenhouse				
S_1P	s^2_g	1.82*	1.75*	0.00
	s^2_e	3.19	2.31	2.24
FSP	s^2_g	2.27*	0.75*	0.50*
	s^2_e	1.35	0.95	0.76
Downy mildew, field-seedling stage				
S_1P	s^2_g	2.47*	1.30*	0.10
	s^2_e	1.26	1.54	1.66
FSP	s^2_g	3.79*	1.44*	0.66*
	s^2_e	2.32	1.40	1.17
Downy mildew, field-adult plants				
S_1P	s^2_g	0.06	0.62*	0.56*
	s^2_e	1.95	1.31	0.76
FSP	s^2_g	1.02*	0.00	0.02*
	s^2_e	2.26	1.14	0.43
Panicle length				
S_1P	s^2_g	3.86*	6.33*	5.63*
	s^2_e	3.50	4.07	3.81
FSP	s^2_g	4.89*	3.14*	3.17*
	s^2_e	3.68	3.04	4.34

* Genotypic variance components larger than twice their error variance

as in the field. The error variances for the S_1P trial in the greenhouse were much higher than those for the FSP trial. This may be due to poorer emergence in the S_1P trials as the mean number of plants per pot was only 17.0, compared to 43.5 for the FSP trial. Under field testing, no differences in emergence were observed, and the error variances were of the same order of magnitude.

Genotypic variances for adult plant resistance to downy mildew were much lower than for seedling resistance, whereas the error variances were in the same order of magnitude as those for seedling resistance in the field. This could be due to sampling effects as there were fewer adult plants than seedlings for determining downy-mildew percentage. Estimates of genotypic variance of S_1P were low. In the C_0, the trial failed to detect significant variation, and later did not show any decrease over cycles, whereas, for FSP, they decreased sharply from the C_1. For both types of progeny, the error variances decreased considerably as the mean number of infected plants decreased (Tables 3, 4).

The correlations for downy-mildew reaction between greenhouse and field results were highly significant ($P < 0.001$), but of only an intermediate level: 0.66 for the FSP and 0.51 for the S_1P for the first count and 0.61 and 0.50 for the second count, respectively. Correlations between the first and the second field counts were a little higher, 0.71 for FSP and 0.62 for the S_1P.

Correlated responses

Selection for seedling resistance to downy mildew in the greenhouse resulted in a significant increase in resistance in the field at the time of flowering (Table 4). This is of particular interest as this material is highly tillering, and carries shoots at a vulnerable stage of growth over an extended period of time. No correlated responses were observed for panicle length, plant height and plant stand. Although the S_1P showed a trend for increases in time to 50% bloom, no such correlated response was observed in evaluating FSP (Table 4).

Table 4: Cycle means from 2 cycles of recurrent selection for downy mildew (DM) resistance in WRajPop 88 for characters observed during field screening of 50 random S_1 (S_1P) and full-sib progenies (FSP)

Character/progeny type	Cycle of selection C_0	C_1	C_2	SE
Adult plant DM resistance (% infected plants)				
FSP	3.60	1.14	0.86	-[1]
S_1P	2.23	1.78	1.08	-
Time to 50% bloom (DAS)				
FSP	53.6	55.1	54.0	0.46
S_1P	56.5	56.9	57.7	0.42
Panicle length (cm)				
FSP	20.3	20.6	20.0	0.26
S_1P	19.4	19.0	19.0	0.25
Plant height (cm)				
FSP	144.5	148.4	144.9	2.30
S_1P	130.5	129.3	133.2	1.99
Plants/m^2				
FSP	12.2	12.3	11.7	0.50
S_1P	13.2	11.3	12.1	0.54

[1] Not applicable because of square-root transformation of data

Discussion

The mechanism and the inheritance of resistance to downy mildew in pearl millet are poorly understood. In India, breakdown of resistance has occurred in several single-cross hybrids (AICPMIP 1991), often with devastating results, whereas broad-based open-pollinated varieties show more stable resistance (Fig. 1). Cultivar-specific pathogen populations have been isolated (Ball et al. 1986, King et al. 1989, Thakur et al. 1992), indicating that the pathogen is highly variable, and responds to selection pressure rapidly. One stratagem to enhance durability of resistance would be to maintain genetic variability for resistance in cultivars, and recurrent selection in broad-based populations may be a means to achieve this. Rattunde and Witcombe (1993) reported that recurrent selection using a field screening procedure (Williams et al. 1981) was successful in maintaining a high level of resistance while improving yield in diverse broad-based populations. Increased resistance to downy mildew through recurrent selection has not been reported for pearl millet.

Resistance to downy mildew is commonly improved by using highly resistant African sources in the composition of breeding populations. Recurrent selection methods are frequently used to stabilize these high levels of resistance (Rattunde and Witcombe 1993). Studies documenting the improvement of downy-mildew resistance in pearl millet populations are not available. The utilization of residual intra-line variability for downy-mildew resistance in susceptible inbred lines has occasionally been successful (Singh et al. 1992). In maize, recurrent selection for resistance to downy mildew caused by *Peronospora* spp. has been successful (León et al. 1993).

The results of this study show that genetic variability for downy-mildew resistance exists in a susceptible population. Recurrent selection was successful in exploiting this variation to improve the level of resistance significantly. In all evaluation trials, the mean disease incidence for progenies from the C_2 was significantly lower than that from the C_0. The mean levels of resistance of the C_2 did not differ significantly from those of the resistant controls, ICMP 423 and 81B (Table 2), whereas the performance of the progenies from the C_0 cycle was most similar

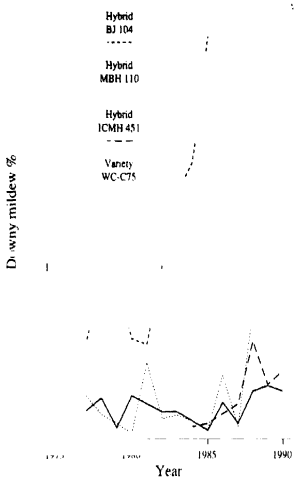

Fig. 1: Downy-mildew incidence (% infested plants) on widely grown pearl millet hybrids and one open-pollinated variety as observed in monitoring nurseries across India from 1975 to 1990 (AICPMIP 1991)

to that of the susceptible inbred control 843B. However, the disease pressure in the evaluation trials is considered to be only moderate. Higher disease levels might have improved the differentiation between the controls and the cycle means, and thus might have allowed a better judgement of the actual level of resistance achieved by this selection scheme.

These results document that recurrent selection based on the modified greenhouse procedure for downy-mildew screening is an effective method of increasing the level of resistance in variable breeding populations of pearl millet. The correlations between greenhouse and field evaluation trials were sufficiently high to indicate that the greenhouse screening predicts field expression of resistance to downy mildew. The correlated field responses to selection in the greenhouse confirm this (Tables 2 and 4). The greenhouse screening method achieved a similar level of differentiation and repeatability (heritabilities on an entry mean basis of 0.53 for S_1P and 0.77 for FSP for the C_0 cycle) as the field screening at the seedling stage (0.80 for S_1P and 0.77 for FSP for the C_0 cycle) with the same material. These findings thus strongly support the usefulness of the modified greenhouse screening method, as the heritabilities and genotypic variances (Table 3), and thus the expected genetic gains, are similar, and it is considerably faster and more flexible in its application than field screening. Predicted correlated gains under field conditions, when selection is carried out in the greenhouse, are expected to be only half those of direct gains because of the intermediate level of correlations between field and greenhouse screening tests.

The rapid decline in genetic variance observed during two cycles of recurrent selection indicates that seedling resistance to downy mildew in this population is controlled by a relatively small number of genes (Geiger and Heun 1989). This is not surprising as this population is relatively narrowly based with respect to sources of genes for resistance to downy mildew. All its parental components originated from the same geographic region where natural disease levels are low. A similar study using a more broadly based pearl-millet population, such as the World Composite from which the highly resistant open-pollinated variety WC-C75 was derived (Fig. 1), is needed to determine whether the selection-induced decline of genetic variation is population dependent. Recurrent selection has been reported to cause rapid decline in genotypic variability for disease and insect resistance in maize (Penny et al. 1967, Jinahyon and Russell 1969, Randle et al. 1984).

However, resistance to downy mildew in maize appears to be governed by a greater number of genes, because evaluation of progress from recurrent selection indicated steady progress over three cycles with no tendency to decline (Khebra et al. 1981, León et al. 1993).

The comparison of variance components indicates that full-sib progenies can be used successfully for improvement of seedling resistance to downy mildew. In pearl millet, full-sib progenies have rarely been used in recurrent selection schemes (Singh et al. 1988, Rattunde and Witcombe 1993). The estimates of genetic variances among the FSP were sufficiently large to predict significant genetic gains from selection. The estimates of error variance (Table 3) from the S_1P and the FSP did not differ much, except in the greenhouse screening where the number of seedlings evaluated for downy-mildew resistance differed markedly for the two types of progeny. In maize, both S_1 progenies (León et al. 1993) and full-sib progenies (Khebra et al. 1981) have been successfully used to improve resistance to downy mildew.

The genotypic variance estimates among the FSP were actually larger than those among the S_1P for downy-mildew resistance, as well as for the other traits measured during the field screening. This is surprising since, theoretically, if gene frequencies are 0.5, the additive genetic variance among the FSP is only expected to be half that of the S_1P (Wricke and Weber 1986). The two types of progeny were tested in different trials, and therefore these results are not fully comparable. However S_1P and FSP trials, both in the greenhouse and in the field, were conducted adjacent to each other at exactly the same time. The same controls were used in both trials, and their means and variances indicate that the testing conditions did not differ in a way expected to change the relative magnitude of the variance components. Schipprack (1993) found similarly high estimates for genotypic variance estimates for the FSP in comparison with the S_1P for days to flowering, panicle length and panicle yield over a wide range of pearl millet composites, with no obvious explanation.

Accidental outcrossing during the production of the S_1P was rejected as an explanation of this observation. The proportion of outcrossed plants within the S_1P in the field trials was not large enough to explain these deviations from theoretical expectations. Comparison of the means of the S_1P and the FSP for plant height, panicle length and time to bloom (Table 4) indicates that inbreeding depression was expressed in the same order of magnitude as was found by Rai et al. (1985), supporting the assumption that the plants were true S_1 progenies.

Visual observations of the field trials suggest that the expression of differences for agronomic characteristics among

the S_1P was reduced because of lower vigour in general, possibly enhanced by the relatively poor growing conditions for millet in the downy-mildew field nursery due to frequent irrigation to promote disease development.

The deviation from the theoretical expectation could also be caused by a high dominance variance component. The degree of dominance has not been studied for downy-mildew resistance. However, the practical experience with crosses among inbred lines is that resistance tends to be dominant over susceptibility (B. S. Talukdar, pers. comm.). For other traits it was found to be relatively small in pearl millet (Vyas and Pokhriyal 1985). The relationship between different types of progeny in pearl millet seems to need more careful study and direct comparison.

Genetic analyses of the resistance to downy mildew in maize in Asia have shown that its inheritance is highly polygenic, and that the additive component of the genetic variance appears to be most important (Kaneko and Aday 1980, Lima et al. 1982 Singhburaudom and Renfro 1982, Borges 1987). The interactions between this host and its parasite appear to be more complex than for pearl-millet downy mildew. Maize is a much more recently introduced crop in Asia and is susceptible to a whole range of tropical downy-mildew pathogens which co-evolved with different indigenous crops (Williams 1984). In different countries, different pathogen species prevail. In sorghum, however, resistance to downy mildew caused by *Peronosclerospora sorghi* (Weston and Uppal) C. G. Shaw appears to be controlled by a few major genes that are mostly dominant (Sifuentes and Frederiksen 1988, Reddy et al. 1992).

This study shows that genotypic variability for downy-mildew resistance exists in the highly susceptible landrace material from northwestern India. Recurrent selection, using a modified greenhouse screening technique based on seedling testing alone, was successful in exploiting this variation, leading to increased resistance and a reduction in genotypic variation after two cycles of selection.

Acknowledgements

The authors acknowledge the help of Barbara Weickel for supervising the greenhouse evaluation experiments, of Dr. S. D. Singh and S. S. Navi for coordinating the selection experiments and the field screening, and of B. Ahmed for producing the full-sib and S_1 progenies. They also thank Dr. H. F. W. Rattunde for his useful comments on earlier versions of the manuscript. Journal Article No. JA 1671

References

AICPMIP, 1975–1991: All India Coordinated (Pearl) Millet Improvement Project, Progress Reports. Indian Council of Agricultural Research, New Delhi, India.

Ball, S. L., D. J. Pike, and C. Y. Burridge, 1986: Characterization of populations of *Sclerospora graminicola*. Ann. Appl. Biol. **108**, 519–526.

Bidinger, F. R., E. Weltzien R., V. Mahalakshmi, S. D. Singh, and K. P. Rao, 1994: Evaluation of landrace top-cross hybrids for arid zone environments. Euphytica (in press).

Borges, O. L., 1987: Diallel analysis of maize resistance to sorghum downy mildew. Crop Sci. **27**, 178–181.

Geiger, H. H., and M. Heun, 1989: Genetics of quantitative resistance to fungal diseases. Annu. Rev. Phytopath. **27**, 317–341.

ICRISAT, 1988: Greenhouse screening for resistance. In: Annual Report 1987, 85–86. Patancheru, A. P. 502 324, India.

Jinahyon, S., and W. A. Russell, 1969: Evaluation of recurrent selection for stalk rot resistance in an open-pollinated variety of maize. Iowa State J. Sci. **43**, 229–237.

Kaneko, K., and B. A. Aday, 1980: Inheritance of resistance to downy mildew of maize, *Peronosclerospora philippinensis*. Crop Sci. **20**, 590–594.

Khehra, A. S., B. S. Dhillon, V. K. Saxena, and N. S. Malhi, 1981: Selection for brown stripe downy mildew resistance in maize. Euphytica **30**, 393–396.

King, S. B., J. Werder, and S. D. Singh, 1989: Pathogenic variation in *Sclerospora graminicola* on pearl millet. Phytopathology **79**, 1390.

León, C. De, G. Granados, R. N. Wedderburn, and S. Pandey, 1993: Simultaneous improvement of downy mildew and agronomic traits in tropical maize. Crop Sci. **33**, 100–102.

Lima, M., J. C. V. A. Pereira, and N. Gemenes-Fernandes, 1982: Introduction of maize (*Zea mays* L.) germplasms as sources for downy mildew (*Peronosclerospora sorghi*) resistance. Maydica **27**, 159–168.

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

Penny, L. H., G. E. Scott, and W. D. Guthrie, 1967: Recurrent selection for European corn borer resistance in maize. Crop Sci. **7**, 407–409.

Pinard, F., 1989: Le mildiou des mils pénicillaires (*Pennisetum americanum* (L.) Leeke) du a *Sclerospora graminicola* (Sacc.) Schroet. Éléments de biologie: étiologie de l'infection, facteurs de résistance foliaire de l'hote, étude in vitro de la virescence. These Doctoral, Univ. Paris-Sud, Centre d'Orsay, France.

Rai, K. N., D. J. Andrews, and V. Suresh Babu, 1985: Inbreeding depression in pearl millet composites. Z. Pflanzenzüchtg. **94**, 201–207.

Randle, W. M., D. W. Davis, and J. V. Groth, 1984: Improvement and genetic control of partial resistance in sweet corn to corn leaf rust. J. Am. Soc. Hort. Sci. **109**, 777–781.

Rattunde, H. F. W., and J. R. Witcombe, 1993: Recurrent selection for increased grain yield and resistance to downy mildew in pearl millet. Plant Breeding **110**, 63–72.

Reddy, B. V. S., L. K. Mughogho, Y. D. Narayana, K. D. Nicodemus, and J. W. Stenhouse, 1992: Inheritance pattern of downy mildew resistance in advanced generations of sorghum. Ann. Appl. Biol. **121**, 249–255.

SAS, 1991: SAS STAT User's Guide, Release 6.03 Edition. SAS Institute Inc., Cary, NC.

Schipprack, W., 1993: Estimation of population parameters and optimization of alternative procedures of recurrent selection in pearl millet (*Pennisetum glaucum* (L.) R.Br.). Diss. Univ. Hohenheim, Stuttgart.

Shetty, H. S., 1987: Biology and epidemiology of downy mildew of pearl millet. Proceedings International Pearl Millet Workshop, 7–11 April 1986, ICRISAT, Patancheru, India, 147–160.

Sifuentes, J., and R. A. Frederiksen, 1988: Inheritance of resistance to pathotypes 1, 2 and 3 of *Peronosclerospora sorghi* in sorghum. Plant Dis. **72**, 332–333.

Singhburaudom, I. N., and B. L. Renfro, 1982: Heritability of resistance in maize to sorghum downy mildew (*Peronosclerospora sorghi* (Weston and Uppal) C. G. Shaw). Crop Prot. **1**, 323–332.

Singh, P., K. N. Rai, J. R. Witcombe, and D. J. Andrews, 1988: Population breeding methods in pearl millet improvement (*Pennisetum americanum*). L'agronomie tropicale **43**, 185–193.

Singh, S. D., and R. Gopinath, 1985: A seedling inoculation procedure for detecting downy mildew resistance. Plant Dis. **69**, 582–584.

———, P. Singh, D. J. Andrews, B. S. Talukdar, and S. B. King, 1992: Reselection of a pearl millet cultivar utilizing residual variability for downy mildew resistance. Plant Breeding **109**, 54–59.

Steel, R. G. D., and J. H. Torrie, 1980: Principles and Procedures of Statistics. McGraw-Hill Book Company, New York, USA.

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

Vyas, K. L., and S. C. Pokhriyal, 1985: Combining ability studies on landraces of pearl millet from Rajasthan. Indian J. Genet. **45**, 247–254.

Wricke, G., and W. E. Weber, 1986: Quantitative Genetics and Selection in Plant Breeding. W. de Gruyter, Berlin, New York.

Williams, R. J., 1984: Downy mildews of tropical cereals. Adv. Plant Pathology **2**, 1–133.

———, S. D. Singh, and M. N. Pawar, 1981: An improved field screening technique for downy mildew resistance in pearl millet. Plant Dis. **65**, 239–241.