RESPONSE OF LOCALLY ADAPTED PEARL MILLET POPULATIONS TO S1 PROGENY RECURRENT SELECTION FOR GRAIN YIELD AND RESISTANCE TO RUST

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ABSTRACT

In the semi-arid zones of Uganda, pearl millet (*Pennisetum glaucum* (L.) R. Br.) is mainly grown for food and income; but rust (*Puccinia substriata* var *indica* (L.) R. Br.) is the main foliar constraint lowering yield. The objective of the study was to genetically improve grain yield and rust resistance of two locally adapted populations (Lam and Omoda), through two cycles of modified phenotypic S_1 progeny recurrent selection. Treatments included three cycles of two locally adapted pearl millet populations, evaluated at three locations. Significant net genetic gain for grain yield (72 and 36%) were achieved in Lam and Omoda populations, respectively. This led to grain yield of 1,047 from 611 kg ha^{-1} in Lam population and 943 from 693 kg ha^{-1} in Omoda population. Significant improvement in rust resistance was achieved in the two populations, with a net genetic gain of -55 and -71% in Lam and Omoda populations, respectively. Rust severity reduced from 30 to 14% in Lam population and from 57 to 17% in Omoda population. Net positive genetic gains of 68 and 8% were also achieved for 1000-grain weight in Lam and Omoda, respectively. Traits with a net negative genetic gain in both populations were days to 50% flowering, days to 50% anthesis, days to 50% physiological maturity, flower-anthesis interval, plant height and leaf area.

Key Words: *Pennisetum glaucum, Puccinia substriata*

RÉSUMÉ

Dans la zones semi-arides en Ouganda, le milet perlé (*Pennisetum glaucum* (L.) R. Br.) est principalement cultivé comme culture vivrière et de rente, mais la maladie de rouille (*Puccinia substriata* var *indica* (L.) R. Br.) est la contrainte majeure affectant le rendement. L'ojectif de l'étude était l'amélioration du rendement en grains et la résistance à la maladie de rouille chez deux populations localement adaptées milet perlé (Lam and Omoda), ceci à travers deux cycles de selection reccurente. Les traitements consistaient à trois cycles de deux populations localement adaptées de milet perlé, évaluées dans trois milieu différents. Un gain genetique significatif de 72 et 36% de rendements en grain a été observe respectivement chez les populations de Lam et de Omoda. Ceci a occasionné des rendements en grains de 1,047 kg ha^{-1} au lieu de 611 kg ha^{-1} chez la population de Lam et 943 kg ha^{-1} au lieu de 693 kg ha^{-1} chez la population de Omoda. Une amélioration significative de la résistance à la maladie de rouille a été obtenue au sein des deux populations, avec des gains génétiques nets de -55 et -71% respectivement chez les populations de Lam et Omoda. La sévérité de la maladie de rouille a été de 30% à 14% au sein de la population de Lam population et de 57% à 17% au sein de la population de Omoda. Un gain génétique positif net de 68 et 8% ont été également obtenu respectivement pour le poid de 1000 grains de Lam et 1000 de Omoda. Les caractères comme le nombre jours à 50% de floraison, le nombre de jours à 50% anthèse, le nombre de jours à 50%

de maturité physiologique, l'intervalle de temps entre la floraison et l'anthèse, la hauteur des plants et la surface des feuilles.

Mots Clés: *Pennisetum glaucum, Puccinia substriata*

INTRODUCTION

Pearl millet (*Pennisetum glaucum* (L.) R. Br.) is an important multipurpose cereal, which performs well under low input environments of Asia and Africa (Izge *et al.*, 2006). It is grown for food, and stover used as cooking fuel, building material or fed to livestock (Vetriventhan *et al.*, 2008; Basavaraj *et al.*, 2010). It is adapted to drought-prone environments, where other cereals hardly survive; thus making it the world's hardiest crop (Reddy *et al.*, 2012). Despite the importance and resilience to adverse conditions, on-farm productivity in Uganda is still low (400-600 kg ha^{-1}) compared with the potential of over 4000 kg ha^{-1} achieved under research environments (Kountche *et al.*, 2013). This is partly due to biotic constraints such as downy mildew (*Sclerospora graminicola* Sacc.), Striga spp., blast (*Pyricularia grisea* (L.) R. Br.), ergot (*Claviceps fusiformis* Loveless.), smut (*Tolyposporium penicillariae* Bref.), rust (*Puccinia substriata* var *indica* (L.) R. Br.,) and birds (Lakshmana *et al.*, 2010).

However, in Uganda rust is one of the major diseases reducing grain yield (Lubadde *et al.*, 2014). The most economical option to control rust is to breed for resistance. However, breeding for monogenic resistance has not been effective because of the multiple races of the pathogen that exist; but developing varieties with many small-effect genes has proved to be the most effective approach to control the disease. This may be achieved through recurrent selection since it leads to accumulation of many small-effect gene loci (Menkir and Kling, 2007). The result is an improved population with maintained genetic variability, which enables response to further improvement (Baskaran *et al.*, 2009).

Recurrent selection has the advantage of increasing the frequency of favourable alleles through additive, partial dominance, dominance or over dominance gene actions. Several recurrent selection schemes have been adopted to improve pearl millet populations. Through full-sib recurrent selection, Bidinger *et al.* (2006) improved grain yield and stover quality; while significant increases in grain yield and striga resistance were achieved through five cycles of both full-sib phenotypic recurrent selection and S$_1$ progeny recurrent selection (Kountche *et al.*, 2013). Although full-sib recurrent selection has the advantage of the improved populations being in their natural highly heterozygous state, there is less probability to identify and move forward desirable recessive alleles compared to S$_1$ progeny recurrent selection (Kountche *et al.*, 2013). The S$_1$ progeny recurrent selection is superior to either half- or full-sib schemes for improving grain yield, because it leads to increased panicle length and surface area (Dutt and Bainiwal, 2005). Basing on this superiority, the phenotypic S$_1$ progeny recurrent selection scheme was adopted to improve two locally adapted populations in Uganda. The objective of this study was to improve grain yield and resistance to rust of two locally adapted and commonly grown pearl millet populations, through two cycles of phenotypic S$_1$ progeny recurrent selection.

MATERIALS AND METHODS

Experimental materials. Two experimental populations (Lam and Omoda) were selected from the predominantly pearl millet growing regions in northern and eastern Uganda. The Lam population was collected from northern; while the Omoda population was collected from eastern Uganda. The populations were described by farmers as being low grain yielding and rust susceptible, but drought tolerant, with good taste. Farmers described Omoda population as short in terms of duration and plant height; while Lam population was tall and late maturing. These traits were the basis for improvement through phenotypic S$_1$ progeny recurrent selection.

Developing cycles. Selection and recombination trials were done at the National Semi-Arid Resources Research Institute (NaSARRI), located in Serere district in eastern Uganda. Approximately 2000 C_0 plants of each population were grown and 500 plants (20% selection pressure) with rust severity of less than 20%, selected from each population and selfed. The selfed seed was bulked and 0.10 ha (20 m x 50 m) plots planted with each population for recombination to form the first cycle (C_1) seed. The modification was to rogue before flowering leaving plants with less than 20% rust severity for recombination. The same procedure was adopted to form cycle two (C_2). A summary of the recurrent selection scheme indicating the time frame is shown in Table 1.

Field evaluation of the cycles. Evaluation of cycles C_0, C_1 and C_2 of the two populations was done in 2014, at three sites; namely Serere (1°32'N, 33°27'E, 1140 metres above sea level), Kitgum (03°132 N, 032°472 E, 969 m.a.s.l) and Katakwi (01°542 N, 034°002 E, 1107 m.a.s.l). The three sites were rust hot-spots and located in areas where pearl millet is predominantly grown. Materials were planted in 20 m x 50 m plots, in a completely randomised block design, with three replicates and 60 cm x 30 cm spacing. Hand weeding was done twice and NPK fertiliser was applied at 40:30:35 kg ha^{-1}, respectively, as recommended by Khairwal *et al*. (2007). The fertiliser was applied in two splits, the first one at sowing and the other 4 weeks after sowing.

Data collection and analysis. Data were collected at 50% physiological maturity on at least 36 plants per plot. The data included; rust severity at 50% physiological maturity, using the modified Cobb's disease severity scale (0-100%); panicle length (Lp cm) and panicle girth (Wp cm) for calculating panicle area (cm^2) using formula (3.14 x Lp x Wp), 1000-grain weight, plant height, days to 50% flowering, days to 50% anthesis, flower-anthesis interval, days to 50% physiological maturity, number of productive tillers, grain yield, harvest index, leaf length and leaf breadth of third leaf from plant top for calculating leaf area . Data analyses were conducted using SAS software, Version 9.2 (SAS Institute. Inc., 2012), where

TABLE 1. Modified S_1 recurrent selection scheme for pearl millet rust resistance study in Uganda

Season	Activity
First season (February - June 2012)	Growing 2000 plants for each population (C_0 populations) and keeping remnant seedInoculation with rust urediniospores Selecting (S_0) and selfing 500 plants (S_1 progeny) showing low severity (10-20%) from each population and bulking the seed
Second season (August - November 2012)	Growing 2000 plants of each population and inoculating with rust urediniospores Rogueing was done before flowering to leave 500 plants with less than 20% rust severity for recombination. Bulking of selected C_0 plants was done to form C_1 seed and remnant seed kept
First season (February - June 2013)	Growing 2000 plants from each of the two C_1 populations Inoculation with rust urediniospores Selecting and selfing 500 plants with less than 20% rust severity to form S_1 progeny
Second season (August - November 2013)	Growing 2000 of S_1 progeny from the C_1 populations and inoculating with rust urediniospores Rogueing before flowering to leave 500 plants with less than 20% rust severity for recombinationBulking seed to form C_2 seed
First season (February - June 2014)	Evaluating the C_0, C_1 and C_2 of each population in three rust hot spot environments (Serere, Kitgum and Katakwi)

analysis of variance for the traits was determined based on Proc GLM using the model:

Y= μ + rep (sites) + sites + cycles + varieties + sites x varieties + varieties x cycles + sites x cycles + random error

Where:

Y = observed value; μ = grand mean; rep/blocking = replication effect with 3 levels; sites = site effect with 3 levels; varieties = effect of varieties; cycle = cycle effect and interaction of cycles, sites and varieties

Response to selection was determined using the means of the cycles C_0, C_1 and C_2 for populations; Broad sense heritability was calculated using the formula; $H^2 = V_g/V_p * 100$:

Where:

H^2 = Broad sense heritability, V_g= genetic variance; V_p= phenotypic variance = (V_g + interaction variances + estimated error mean square); μ_{C0}= mean for C_0; μ_{C1}= mean for C_1; μ_{C2}= mean for C_2.

Gain per cycle was determined using differences between cycle means as:

$(\mu_{C2} - \mu_{C0})$, $(\mu_{C2} - \mu_{C1})$, $(\mu_{C1} - \mu_{C0})$

RESULTS AND DISCUSSION

Analysis of variance of the cycles. Sites had no significant effect on grain yield (GY) and four other traits (flower-anthesis interval (FAI), days to 50% physiological maturity (PSM_{50}), plant height (PLH) and number of productive tillers (PRT0) but were important for rust severity (RUST), flowering days (FLO_{50}), anthesis days (ANT_{50}), panicle area (PAR), leaf area (LAR), harvest index (HI) and 1000-grain weight (TGW) (Table 2). The main effects of cycles and populations were significantly important for all the traits. In addition, the interactions involving the cycles, populations and sites were significantly (P<0.05) important for GY and RUST and five other traits. The variation of cycles and populations in response to GY, RUST and other traits across sites may be attributed to genetic differences in the base populations used in this study. Such variation was also reported by Dutt and Nirania (2005), who worked at Chaudhary Charan Singh, Haryana Agricultural University, Hisar-India. Unlike in this study, they reported significant differences in cycle for GY, PRT and PLH when they compared various schemes of recurrent selection. Likewise, Bidinger *et al.* (2006) reported no significant effects of cycles for PAR and HI, thus contrasting with our study findings.

The variation of cycles and populations in trait response may be due to the genetic differences in base populations (Table 3), as seen for Omoda population. The variation in response to selection indicates a possibility to improve the traits through phenotypic S_1 progeny recurrent selection (Bidinger *et al.*, 2006). This observation was also reported by Kannan *et al.* (2014) in their study to quantify response to recurrent selection for grain yield and related traits using SSR markers. They noted that the possibility was due to pearl millet being a highly cross-pollinating crop, with a high level of genetic variability. The significant effect of cycles and populations on GY and RUST also shows the suitability of the phenotypic S_1 progeny recurrent selection to improve the quantitative traits (Hallauer and Darrah, 2008). The improvement can be achieved in diverse environments, with minimal antagonistic interaction (Bidinger and Raju, 2000).

Individual populations had varying response to selection (Table 4). In Lam population, the effect of cycles led to increase in grain yield of 436.50 kg ha^{-1}. The observed increase in grain yield was due to cumulative improvement in TGW, PRT, HI and improved rust resistance. The rust resistance increased through the increase of favourable genes as a result of selection, which largely depends on the quality of the population being improved. The response to selection also had negative significant effects on many traits in the study populations (Table 5).

Broad sense heritability estimates (Table 3) were relatively high for GY, RUST, FLO_{50}, ANT_{50}, TGW for the populations; an indicator that the phenotypic S_1 progeny recurrent selection was effective in improving these populations.

TABLE 2. Mean squares for analysis of variance for Lam and Omoda pearl millet populations in Uganda

Source	DF	GY	RUST	FLO_{50}	ANT_{50}	FAI	PSM_{50}	PLH	PRT	PAR	LAR	TGW	HI
Sites	2	34516.48ns	169.72*	29.97**	24.34**	0.41ns	6.35ns	58.32ns	0.36ns	2454.46*	32392.93*	1.35*	73.85*
Rep(site)	6	25601.89ns	34.94*	1.07ns	0.62ns	1.11*	5.89ns	59.41ns	4.33ns	767.13*	6440.34ns	0.34ns	21.36ns
Cycle	2	539185.32**	4049.58**	1218.29**	1346.35**	3.21*	1261.91**	19162.01**	14.75*	1181.70*	311315.33**	23.86**	53.68*
Populations	1	7921.15*	2092.66**	10660.58**	11545.71**	17.66**	48631.81**	198852.00**	17.77*	54075.93**	2708272.14**	179.02**	343.12**
Variety*cycle	2	41223.95*	719.19**	259.12**	307.68**	2.25*	515.18**	10164.46**	100.62**	136.619ns	80857.41**	14.91**	102.47*
Sites*cycle	4	31076.57*	28.29ns	40.54**	46.24**	0.22ns	82.55*	44.31ns	0.87ns	899.92*	4116.23ns	0.65ns	14.76ns
Sites* populations	2	44506.15ns	58.14*	0.15ns	0.01ns	0.18ns	57.83ns	409.02*	10.77*	1647.40*	11363.98ns	0.39ns	6.68ns
Sites* populations *cycle	4	5355.92*	46.16*	3.47*	4.73*	0.87ns	177.26**	80.83ns	7.28ns	1057.23*	17267.05*	0.29ns	
Error	30	41580.04	15.69	0.99	1.12	0.49	5.62	81.36	4.03	342.97	5558.34	0.56	20.41
Rsquare		56.59	96.40	99.79	99.78	73.51	99.69	99.07	73.16	88.26	95.69	94.08	63.78
CV (%)		25.14	15.07	1.21	1.23	19.47	1.88	4.02	23.53	13.34	10.96	8.62	38.62
SD		203.91	3.96	0.99	1.06	0.7	2.37	9.02	2.01	18.52	74.55	0.73	4.52
Grand mean		811.05	26.28	82.43	86.03	3.59	126.42	224.48	8.53	138.78	680.35	8.66	11.70

Testing done at α = 0.05, * = significant P<0.05, * = significant P<0.0001, ns = non-significant P>0.05. GY = grain yield (kg plant^{-1}), RUST = rust severity at 50% physiological maturity, FLO_{50} = days to 50% flowering, ANT_{50} = days to 50% anthesis, FAI = flower-anthesis interval (days), PSM_{50} = days to 50% physiological maturity, PLH = plant height (cm), PRT = number of productive tillers, PAR = panicle area (cm^2), LAR = leaf area (cm^2), TGW =t housand grain weight (g), HI = %harvest index

TABLE 3. Estimates for genetic variance, phenotypic variance and broad sense heritability for Lam and Omoda pearl millet populations in Uganda

Variance	GY	RUST	FLO_{50}	ANT_{50}	FAI	PSM_{50}	PLH	PRT	PAR	LAR	TGW	HI
Lam												
Vg	429526.4	678.33	1297.21	1468.22	5.39	1694.16	28549.41	72.15	1055.5	352848.1	36.13	121.87
VP	578630.1	751.66	1327.67	1497.85	8.74	1948.18	28898.92	91.37	3207.84	387091.4	38.34	193.4
(%H²)	74.23	90.24	97.71	98.02	61.62	86.96	98.79	78.96	32.9	91.15	94.26	63.02
Omoda												
Vg	150882.9	4090.45	180.21	185.8	0.07	82.93	777.05	43.22	262.81	39324.63	2.64	34.28
VP	267236.2	4394.79	227.63	235.81	1.28	177.84	1322.49	60.06	5942.46	93271.01	5.04	165.44
(%H²)	56.46	93.08	79.17	78.79	5.49	46.63	58.76	71.96	4.42	42.16	52.31	20.72

GY = grain yield (kg plant-1), RUST = rust severity at 50% physiological maturity, FLO_{50} = days to 50% flowering, ANT_{50} = days to 50% anthesis, FAI = flower-anthesis interval (days), PSM_{50} = days to 50% physiological maturity, PLH = plant height (cm), PRT = number of productive tillers, PAR = panicle area (cm²), LAR = leaf area (cm²), TGW = thousand grain weight (g), HI =%harvest index

However, the low heritability estimates achieved for FAI, PAR and HI in Omoda population shows that these traits needed more than two selection cycles for improvement; the low heritability being an indicator for a possibility for genetic improvement through recurrent selection. The high heritability estimates imply that for most of the traits, the phenotypic variation observed was mainly due to genetic effects; an indicator that these traits may be improved in diverse environments as also noted by Abuali *et al.* (2012) and Ezeaku and Mohammed (2006).

The high heritability estimates have been reported for many traits. Dutt and Bainiwal (2005) reported high heritability estimates of 80 and 53% for GY and PAR, respectively. In addition, high broad sense heritability estimates have been reported for panicle dimensions (Varu *et al.*, 2005); while Kountche *et al.* (2013) reported a 71% heritability estimate for days to 50% flowering after five cycles of recurrent selection; although in this study more than 79% was achieved after only two cycles of recurrent selection. However, for GY, Bidinger and Raju (2000) reported low heritability estimates of 16%. The high broad sense heritability for TGW was also reported by Borkhataria *et al.* (2005) and Solanki *et al.* (2002), although Sachan and Singh (2001) reported moderate broad sense heritability for the same trait. Therefore, findings from the current study are consistent with some previous investigations.

Performance of the cycles. Grain yield for the cycles for the two populations were significantly different across locations; where C_2 performed better than C_1 and C_0 (Table 4). This indicates a positive response to phenotypic S_1 progeny recurrent selection. Lam population had grain yield improved from 611 to 1,047 kg ha-1, compared with Omoda, which had a mean grain yield improved from 693 to 943 kg ha-1. Bidinger and Raju (2000) reported that if high genetic variation exists in selected progeny, increase in grain yield may be due to recombination effects of the cycles. However, in our study the highest grain yield attained was still low compared with the potential of over 4000 kg ha-1 recorded by Kountche *et al.* (2013) after five cycles of recurrent selection. This implies that further improvement in grain yield may be possible through more selection cycles.

TABLE 4. Means for selected traits of cycles for Lam and Omoda pearl millet populations

Traits	Lam					Omoda				
	C_2	C_1	C_0	Standard error	$LSD_{(0.05)}$	C_2	C_1	C_0	Standard error	$LSD_{(0.05)}$
GY	1047.10a	811.70b	610.60b	280.13	287.72	943.10a	761.18b	692.54b	70.91	72.83
RUST	13.45a	16.83a	29.89b	5.00	5.14	16.76a	23.99b	56.77c	3.60	3.70
FLO_{50}	85.22a	95.11b	109.12c	0.97	1.00	64.61a	67.22b	73.32c	1.15	1.19
ANT_{50}	88.74a	99.07b	114.14c	0.92	0.95	67.52a	70.29b	76.40c	1.02	1.04
FAI	3.52a	3.96a	5.02b	0.68	0.70	2.92a	3.07a	3.08a	0.46	0.47
PSM_{50}	141.10a	160.64b	167.55c	2.19	2.25	92.95a	97.63b	98.64b	2.07	2.12
PLH	222.52a	301.33b	331.63c	11.18	11.48	154.78a	163.27b	173.34c	6.23	6.39
TOT	13.82a	12.53a	13.06a	2.24	2.3	7.87a	8.16a	12.27b	1.69	1.74
PRT	12.37a	7.49b	7.45b	2.08	2.14	6.02a	7.51a	10.34b	1.83	1.88
PRO	89.11a	59.68b	57.51b	7.32	7.52	77.35a	85.35ab	91.65b	12.51	12.85
PAR	158.67a	179.99ab	172.63b	16.04	16.48	112.37a	107.46a	101.58a	21.25	21.83
LAR	675.81a	1025.73b	1011.34b	80.23	82.41	381.21a	482.63b	505.36b	68.89	70.76
1000 GWT	9.14a	5.95b	5.44b	0.58	0.6	10.70ab	10.89a	9.87b	0.93	0.95
BY	0.42a	0.52b	0.59b	0.08	0.09	0.21a	0.20a	0.28b	0.04	0.04
HI	13.04a	8.77b	5.72b	3.3	3.39	14.31a	12.22a	16.12a	4.88	5.01

Means with the same letter are not significantly different at P = 0.05; C_0, C_1 and C_2 are cycles for the base populations, cycle 1 and cycle 2. GY = grain yield (kg plant[-1]), RUST = rust severity at 50% physiological maturity, FLO_{50} = days to 50% flowering, ANT_{50} = days to 50% anthesis, FAI = flower-anthesis interval (days), PSM_{50} = days to 50% physiological maturity, PLH = plant height (cm), TOT = total number of tillers, PRT = number of productive tillers, PRO = %productive tillers, PAR = panicle area (cm^2), LAR = leaf area (cm^2), TGW = thousand grain weight (g), BY = biological yield (kg plant[-1]), HI = %harvest index

TABLE 5. Genetic gain for Lam and Omoda pearl millet populations in Uganda

Trait	Lam population						Omoda population					
	Response to selection			Genetic gain			Response to selection			Genetic gain		
	C2-C1	C1-C0	Net response C2-C0	(C2-C1)/ C0*100	(C1-C0)/ C0*100	Net gain (C2-C0)/ C0*100	C2-C1	C1-C0	Net response C2-C0	(C2-C1)/ C0*100	(C1-C0)/ C0*100	Net gain (C2-C0)/ C0*100
GY	235.40	201.10	436.50	29.00	32.94	71.49	181.92	68.64	250.56	23.90	9.91	36.18
RUST	-3.38	-13.06	-16.44	-20.06	-43.70	-55.00	-7.23	-32.78	-40.01	-30.13	-57.74	-70.47
FLO_{50}	-9.89	-14.01	-23.89	-10.40	-12.84	-21.90	-2.62	-6.10	-8.72	-3.90	-8.32	-11.89
ANT_{50}	-10.33	-15.07	-25.39	-10.43	-13.20	-22.25	-2.77	-6.11	-8.88	-3.94	-8.00	-11.62
FAI	-0.44	-1.07	-1.50	-11.10	-21.22	-29.96	-0.15	-0.01	-0.16	-4.79	-0.40	-5.16
PSM_{50}	-19.54	-6.91	-26.45	-12.17	-4.13	-15.79	-4.68	-1.01	-5.69	-4.80	-1.02	-5.77
PLH	-78.81	-30.30	-109.11	-26.15	-9.14	-32.90	-8.48	-10.08	-18.56	-5.20	-5.81	-10.71
PRT	4.88	0.04	4.92	65.22	0.52	66.09	-1.49	-2.83	-4.32	-19.82	-27.34	-41.74
PAR	-21.32	7.36	-13.97	-11.85	4.26	-8.09	4.91	5.88	10.80	4.57	5.79	10.62
LAR	-349.92	14.39	-335.53	-34.11	1.42	-33.18	-101.42	-22.73	-124.15	-21.01	-4.50	-24.57
TGW	3.19	0.51	3.70	53.55	9.40	67.97	-0.19	1.02	0.83	-1.74	10.31	8.40
H I	4.28	3.05	7.33	48.77	53.31	128.28	2.09	-3.90	-1.81	17.07	-24.19	-11.25

GY = grain yield (kg ha^{-1}), RUST = rust severity at 50% physiological maturity, FLO_{50}= days to 50% flowering, ANT_{50}= days to 50% anthesis, FAI = flower-anthesis interval (days), PSM_{50}= days to 50% physiological maturity, PLH = plant height (cm), PR T= number of productive tillers, PAR = panicle area (cm^2), LAR = leaf area (cm^2), TGW = thousand grain weight (g), HI = %harvest index

But further selection for grain yield should be done concurrently with selection for rust resistance as the mean rust severity attained after two cycles was still above the resistance severity level of less than 10% in both populations. In the present study, rust severity was reduced to 14% from about 30% recorded in the base population for Lam; while a reduction to 16.8% rust severity from 57% was observed in the Omoda population. This shows an improvement in rust resistance attained through the two cycles of phenotypic S$_1$ progeny recurrent selection.

Genetic gains per cycle. A net positive genetic gain for GY (72 and 36%) and TGW (68 and 8%) was achieved, while a net genetic loss was attained for FLO$_{50}$ (-10 and -12%) and PLH (-33 and -11%), respectively (Table 5), in Lam and Omoda populations. The results differ from those reported by Dutt and Bainiwal (2005) where a 20% genetic gain was achieved for GY when they compared cycles of various schemes of recurrent selection at Chaudhary Charan Singh, Haryana Agricultural University, Hisar-India. Dutt and Bainiwal (2005) further reported a genetic gain of 21% for PAR; while in this study a net negative genetic gain of 8% and net positive genetic gain of 11% was recorded for Lam and Omoda populations, respectively. For TGW, a high genetic gain of 68% was reported in Lam population; while a much lower gain (8%) was achieved for Omoda population; showing variation in response to selection in the two populations. This further emphasises the importance of phenotypic S$_1$ progeny recurrent selection as an effective scheme for improving pearl millet populations. A negative net genetic gain for rust resistance was achieved in both populations; indicating a genetic improvement for rust resistance through selection. A positive net genetic gain was achieved in the Lam population for PRT and HI (Table 5); while a net genetic loss was realised in the Omoda population for the same traits. In addition, the two cycles of selection resulted in a net genetic loss in both populations for FLO$_{50}$, ANT$_{50}$, FAI, PSM$_{50}$, PLH, and LAR; an indicator that, through selection, some traits may be improved while a loss may occur in others. The loss in genetic gain

may be attributed to the effect of inbreeding depression due to selfing. In addition, the rapid change in genetic gain for GY and RUST after two cycles of selection indicates that the two traits were controlled by a relatively large number of small effect genes.

CONCLUSION

Significant increases in grain yield and rust resistance are achieved through two cycles of phenotypic S$_1$ progeny recurrent selection. Results show that genetic variability exists for low grain yield in the rust susceptible populations and phenotypic S$_1$ progeny recurrent selection may effectively be exploited to improve the yield and resistance to rust in locally adapted pearl millet populations. The improvement in the grain yield, rust resistance and other yield-related traits is reflected in the significant desirable genetic gains observed. The improvement in grain yield and rust resistance is further confirmed by the higher grain yield and lower rust severity achieved in the second cycle of selection. This is an indicator that through the two cycles of phenotypic S$_1$ recurrent selection genetic improvement for grain yield and rust resistance is achievable. However, higher broad sense heritability estimates are evident in the Lam population relative to Omoda population. This indicates that the two populations have differing potential for genetic improvement. In addition, low heritability is registered for traits like flower-anthesis interval, panicle area and harvest index in Omoda population; implying that these traits needed more cycles of recurrent selection to achieve better genetic improvement. A rapid change in genetic gain for grain yield and rust resistance and other traits, after two cycles of selection, in the two populations indicates that the phenotypic S$_1$ progeny recurrent selection is effective in achieving genetic improvement of the two traits and thus improving rust resistance and grain yield of the two locally adapted populations Lam and Omoda. Results from this study also show that response to recurrent selection depends on the genetic back ground of the population and the target traits.

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