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Comparing decentralized participatory breeding with on-station conventional sorghum breeding in Nicaragua: I. Agronomic performance

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ABSTRACT

Few studies have assessed the effective gains achieved by collaborative decentralized participatory breeding, in terms of yield and other agronomic traits, in comparison with centralized conventional breeding using the same breeding schemes. Our study concerned an experience of participatory improvement of *tortillero* sorghum for low-input cropping systems in northern Nicaragua. It set out to compare the effect of two breeding schemes simultaneously managed on-station and on-farm. Two synthetic populations were used as sources of genetic variability. The study was designed to distinguish between three "selection modes": farmers' selection on-farm (FoF), breeder' selection on-station (BoS) and breeder's selection on-farm (BoF). After two selection cycles, we found that FoF selection reduced phenotypic variability as much as BoS selection. In general, BoS selection produced higher-yielding lines under the target on-farm conditions. But FoF selection was more effective in promoting lines with higher values for an index of agronomic suitability (IAS), expressing a better balance between earliness, plant height, grain size and yield. Such genotypes might cope more easily with local environmental constraints and farmers' preferences. BoF selection did not prove to be effective for either yield or IAS. This research shows the need for close collaboration between farmers and breeders as well as complementarities between the selection phases managed on-farm and on-station, to make breeding for difficult environments fully efficient.

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1. Introduction

Participatory breeding has been suggested as an effective strategy for developing varieties combining productivity gains, adaptation to particular cropping systems and quality traits for subsistence agriculture in marginal environments. This approach emerged in the late 1980s and early 1990s (Maurya et al., 1988; Sperling et al., 1993), and has been widely implemented over the last decade in various social contexts and physical environments. Until now, most experiences described in the literature have referred to participatory varietal selection (PVS), i.e. participatory evaluation and selection of fixed or almost fixed genetic material. In various crops and contexts, PVS has proved to be efficient for (i)

quick identification of new varieties which perform well under the target stress conditions and show high farmer acceptance, (ii) faster release and greater adoption by farmers of these varieties, and (iii) being more cost-effective, when compared to conventional breeding (FB) programmes (Joshi et al., 1997; Mulatu and Belete, 2001; Ceccarelli and Grando, 2007; Tiwari et al., 2009).

There are still few examples of participatory selection in segregating populations, known as participatory plant breeding *sensu stricto* (PPB). Using the typology proposed by Biggs (1989), the way farmers participate in these programmes is often collaborative, in some cases it is collegial or consultative. In a majority of documented PPB programmes, farmers have been involved at an advanced stage (F₅ to F₇) in the actual breeding process (i.e. selection work in segregating generations), after previous and *presumably not intensive* selection by breeders, as described for rice (Sthapit et al., 1996; Joshi et al., 2007; Gyawali et al., 2007). Nevertheless, the number of PPB programmes involving farmers in the early segregating generations has increased in the last decade. Of them, several interesting experiences were conducted in Latin America with resource-poor farmers in marginal environments; the breeding schemes were commonly developed from crosses

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between “criolla” cultivars and exotic lines bringing disease resistance, and decentralized farmers' selection started in the F₂ to F₄ generations or equivalent, as was done in Nicaragua (Almekinders et al., 2006), Costa Rica (Araya-Villalobos and Hernández-Fonseca, 2006), Honduras (Rosas et al., 2003) or Colombia (Kornegay et al., 1996). Nevertheless, except for the last case, these works published in Spanish are generally not cited in the Anglophone literature. In other still rare PPB programmes, farmers participated in the selection process from the earliest stages, exploring broader genetic variability, as illustrated for maize in India (Virk et al., 2005), cotton in Benin (Lançon et al., 2004), sorghum in Burkina Faso (vom Brocke et al., 2008) or cassava in Ghana (Manu-Aduening et al., 2006).

In such collaborative works, it was often difficult to distinguish between the effect of farmers' selection and environmental effects, and generally it was not designed to allow effective comparisons with breeders' selection. Analysing the results of several collaborative plant breeding programmes, Witcombe et al. (2006) concluded that to achieve highly client-oriented breeding, farmers' participation in plant selection in segregating generations should be considered as an option, not a principle, unless the main objective was farmer empowerment. Based on selection theory, Atlin et al. (2001) argued that effectiveness of any selection environment is determined by both the genetic correlation between genotype performance in the selection and target environments and the heritability of genotypic differences in the selection environment. Based on both selection theory and two case studies on maize and wheat, Bänziger and Cooper (2001) concluded that significant productivity gains under low-input conditions could be better achieved with formal breeding programmes, when the breeders make use of appropriate genetic variation, multi-environment trials data representative of the main stress factors, and indirect selection for adequate secondary traits. In this case, farmers should play a major role in identifying target selection environments, evaluating the germplasm under selected stress conditions and balancing the various qualitative and quantitative traits considered for adaptation in each target environment. For these authors, on-farm farmers' selection alone cannot identify the best genotypes with the expected trait combinations for these stressful environments, subjected to large genotype × site × year interactions. However, after an extensive review of the literature, Dawson et al. (2008) concluded that breeding programmes for low external-input cropping systems are more efficient when decentralized and when they involve farmers at the early stages of selection.

In Nicaragua, from 2005 to 2008, breeders, agronomists and local farmer groups implemented simultaneous on-station and on-farm breeding schemes on tortillero sorghum. White-grain sorghum is an important staple crop for the drought-prone areas of Central America (CA), particularly for the CA dry belt, extending from Nicaragua to Guatemala. Food sorghums, to be distinguished from red-grain industrial sorghum produced for the poultry industry, are commonly separated into millón (photoperiod-sensitive) and tortillero (early insensitive) types. In Nicaragua, both types are mainly produced by resource-poor farmers under low-input cropping systems in marginal areas including hillsides. Yields are generally low and highly variable depending on the annual rainfall and field fertility. Given the poor agronomic performances under such stressful conditions, deficient grain and fodder quality and ill-adapted seed distribution strategies, the adoption rate for the national modern tortillero varieties remains very low (Trouche et al., 2006). Decentralized participatory variety selection research managed with local NGOs and farmer groups in the northern and central regions from 2002 to 2006 led to the identification of several tortillero varieties of West African origin that performed well and were well accepted, of which Blanco Tortillero was the first to be released at the end of 2007 (Trouche et al., 2009). However, from 2003 to 2004, some leading farmers and the main NGO partner

expressed their interest in creating new sorghum varieties, aiming at better adaptation to particular cropping systems or a better combination of appropriate grain and fodder quality traits with productivity and earliness. For the research team, it was an opportunity for developing and testing breeding strategies and tools adapted to farmer participation, based on concrete queries.

This paper compares the results of three selection modes, i.e. on-farm farmers' selection (FoF), on-station breeder's selection (BoS) and on-farm breeder's selection (BoF). These selection modes were applied to two breeding populations designed for developing improved tortillero varieties for two main sorghum ecosystems of northern Nicaragua. The same senior sorghum breeder carried out selection either on-station or on-farm, while small farmer groups carried out selection on-farm. The effect of the three selection modes were analysed regarding four issues:

- Phenotypic variability
- Gains for agronomic traits and yield
- Yield stability
- Combination of traits

A second publication will analyse the gains achieved in farmers' acceptance and overall performance of the same selection modes.

2. Materials and methods

2.1. Target and breeding environments

The two target areas considered in this study were located in the northern region of Nicaragua, where the research project could develop a strong and stable partnership with locally organized farmer groups and the Cipres NGO (Trouche et al., 2009). The Totogalpa area (13°33'N, 86°29'W, altitude 750–800 m) is home to two of the sites where the sorghum project started its activities in 2002 after intensive diagnostic work (Martínez Sánchez, 2003). This hill-sides area corresponds to manual cropping systems under highly vulnerable conditions, where crops face two major constraints: low soil fertility and recurrent drought (average rainfall lower than 800 mm with high intra-season and inter-annual variability). The Pueblo Nuevo area (13°23'N, 86°29'W, 600 m) was added to the research project in the course of its third year, in response to a Cipres and Cosenu local farmer organization request for suitable dual purpose (grain and forage) varieties for this zone. This area is characterized by fairly fertile soils and more favourable rainfall conditions (800–1000 mm) as well as an intermediate degree of intensification (use of animal traction for land preparation).

The selection work was conducted in a farmer's field located in each of the target areas, as well as at the Centro Nacional de Investigación Agropecuaria (CNIA) (12°08'N, 86°10'W, altitude 56 m), near Managua and about 200 km from the on-farm sites. The on-farm fields were owned and managed by members of a regional network of sorghum and bean research farmers. The sorghum research programme of the Instituto Nacional de Tecnología Agropecuaria (INTA) is based at CNIA, which hosts most of the breeding and early evaluation work. The environmental conditions (average annual rainfall = 1230 mm, fertile deep soils, high leaf disease incidence) and cultural practices applied for sorghum experimentation differ significantly from the common growing conditions of tortillero sorghum.

2.2. Breeding goals

An iterative interaction process between the local farmer groups and the research team led to the identification of breeding goals and selection criteria, as described by Trouche et al. (2009). At each

Table 1

Selection criteria defined by the participant farmer-breeders for the Totogalpa and Pueblo Nuevo target areas.

Target area	Breeding population	Selection criteria
Totogalpa area	PCR-1	Early (60 days to flowering and 90 days to maturity), drought tolerance, adaptation to low soil fertility, yield stability and enhanced yield, good grain appearance for the local market and high quality for tortilla (white semi-vitreous large grains)
Pueblo Nuevo area	PCR-2	Intermediate cycle (70 days to flowering and 100–105 days to maturity), adaptation to intermediate soil fertility, height = 1.5–1.8 m, improved fodder quality, high grain yield, grain appearance for the local market (including poultry) and high quality for tortilla (white semi-vitreous large grains)

on-farm breeding site, selection criteria were refined through a discussion between the future farmer breeders and the research team (Table 1).

2.3. Genetic material

Two synthetic populations segregating for the ms_3 genetic male-sterility gene, PCR-1 and PCR-2, were used as the source of genetic variability to implement the two breeding schemes. PCR-1 was created for grain production in unfavourable environments characterized by drought stress and low soil fertility. PCR-2 was developed for dual purpose production in semi-favourable agro-climatic conditions.

The PCR-1 population was created by the introgression of six elite lines, chosen as having one or two important traits for the target environment and/or production goal (Table 2), associated with good agronomic adaptation and acceptance by farmers, identified from the previous PVS phase. We used synthetic population PP34 from Purdue University as the source of the ms_3 male-sterility gene. Seeds of this population were provided by R. Clara, coordinator of the Intormil Central America programme based in El Salvador, where the population underwent several cycles of random mating. Introgression crosses were produced on-station during the 2004 off-season between male-sterile (MS) plants (genetically $ms_3 ms_3$) identified in PP34 and each selected parental variety, used as male. In the fertile F_1 generation, six plants per cross were self-pollinated and then harvested in bulk to obtain F_2 seeds. After threshing, seeds of the 2–3 F_2 s progenies derived from a specific parent were equally bulked, and the six mono-parent bulks chosen were then equally mixed to produce PCR-1 initial bulk as detailed in Table 2. This bulk was planted on-station during the 2005 off-season in an isolated plot of approximately 3000 plants, for random intercrossing through open-pollination. At maturity, 250 MS plants previously tagged at anthesis were harvested, discarding plants showing very poor phenotype, and individually threshed. The base population PCR-1 was formed by bulking 10 g of seeds from each of the chosen MS plants. The PCR-2 population was created from the introgression of six other elite lines (Table 2), using the same method and agenda described for PCR-1.

2.4. Breeding schemes and selection modes

The breeding schemes developed on-station and on-farm for each population are described in Fig. 1. Initially both schemes were designed to distinguish the three selection modes previously defined: on-farm farmers' selection (FoF), on-station breeder's selection (BoS) and on-farm breeder's selection (BoF). Unfortunately for the PCR-2 population, the S_1 progenies derived from the

BoF selection mode were lost during the 2006 rainy season because of a very severe drought.

The breeder was a professional sorghum breeder with about 20 years' experience in sorghum breeding in tropical environments (West Africa and Central America). The farmer-breeders (FBs) were experienced farming men and women, involved in the research activities conducted during the PVS phase, chosen for having the necessary skills for performing a selection work: good knowledge of the crop, high aptitude for observation and trait evaluation, and great motivation for this project. All were resource-poor farmers with similar social profiles.

The PCR-1 and PCR-2 populations (S_0 generation) were planted during the 2005 *postrera*¹ rainy season, both at the CNIA station and in a farmer's field, using similar plot sizes and seed quantities. FBs were given a training course on the principles of genetics and plant breeding, as well as indications of the heritability of the main traits under selection. Before each selection cycle, they were invited to reconfirm the selection criteria in order to make sure they maintained constant selection pressure throughout the process. Following these criteria, three FBs at Totogalpa and four FBs at Pueblo Nuevo carried out their own selection along with the professional breeder, but independently, with the breeder tagging "his" selected plants after the farmers to avoid influencing them. On the research station, the breeder used the same selection criteria and applied the same selection intensity as those used at the corresponding on-farm site. Table 3 summarizes the total number of plants used in the S_0 generation, the number of selected plant-progenies at the S_1 and S_2 generation stages, and selection intensity.

From the S_1 s to S_3 s generations, breeding work was consistently carried out by the same breeder and FBs. In the S_1 and S_2 generations, common selection pressure was exerted by both the breeder and the FBs, although less strictly by the FBs: about 40% of the less attractive progenies were completely discarded, one to two plants were selected in the 40% "acceptable to good" progenies and four to five plants in the top 20% progenies.

From 2005 to 2007, the rainy seasons were highly contrasting, for both the total amount of rain and rainfall distribution, particularly at the on-farm breeding sites. At Totogalpa and Pueblo Nuevo, the *postrera* rainy season was very wet in 2005 and 2007 (420–700 mm and 540–630 mm respectively) while very dry in 2006 (190 and 300 mm, respectively).

2.5. Evaluation of the progenies for yield and other agronomic traits

Yield trials were set up during the 2007 and 2008 *postrera* season at the CNIA station (for both populations) and at the on-farm breeding locations (Totogalpa for PCR-1 and Pueblo Nuevo for PCR-2) to assess the agronomic performance of the lines derived from the three selection modes.

In 2007, the PCR-1 trials included 30 lines from each selection mode, representing the 10% top lines according to the 2006 evaluation, and a random 50% of the remaining progenies, and four released varieties or elite lines used as controls. The PCR-2 trials included 60 lines from each selection mode, the 10% top lines of the 2006 evaluation, a random 40% of the remaining progenies, and four controls.

The 2008 trials evaluated the 20% top lines for each selection mode, according to a *global* selection index integrating agronomic performance (the IAS index further explained) and farmer (for on-farm selection) or breeder acceptance (for on-station selection).

¹ Second rainy season (August–November) when tortillero sorghum is mainly grown.

Table 2
Parents of the PCR-1 and PCR-2 populations with their relative contribution.

Synthetic population	Parent	Criteria of choice	% of each parent in the population
PCR-1	CIRAD 438	Short plant height, panicle shape, tan plant colour	8.3
	BF 94-6/41K-2F-1K-2K	Midge resistant, earliness	8.3
	BF 96-2/46-1K-1K-1K	Midge resistant, stay green, and fodder quality	8.3
	CIRAD 437	Earliness, high yield potential, disease resistance	8.3
	BF 89-12/1-1-1 (CIRAD 492)	Grain appearance (intense white colour) and weight, drought tolerance, tan plant colour	8.3
	INTA Ligero	Short plant height, grain size, high leaf/stem ratio	8.3
	PP34 (population source of <i>ms₃</i> gene)	Pre-adapted population, good grain quality	50
PCR-2	BF 94-6/46K-1K-1K-1F	Midge resistant, short plant height, good panicle exertion, sweet stems	8.3
	BF 96-2/56-1K-2K-1K	Midge resistant, tan plant colour	8.3
	BF 89-18/133-2-1	Grain aspect (colour and texture) and weight, high yield potential and stability	8.3
	Africana	Yield stability, good plant type with high leaf/stem ratio	8.3
	INTA CNIA	Broad adaptation, panicle shape	8.3
	ICSR 20	Good plant type, disease resistance, fodder quality	8.3
	PP34 (population source of <i>ms₃</i> gene)	Pre-adapted population, good grain quality	50

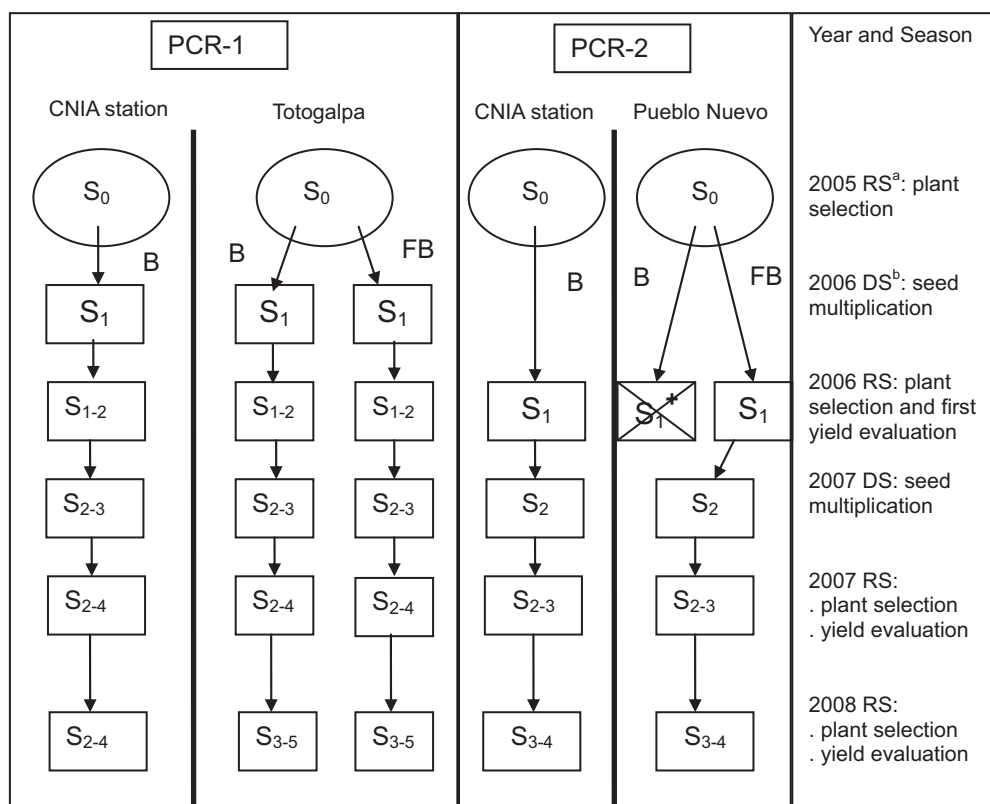
These trials were set up again in their respective on-farm and on-station breeding environments, as well as at a second on-farm site.

Alpha-lattice designs with three replications were used for these evaluation trials. For each genotype, the harvested plot sizes were generally of 4–8 m² (2 or 3 rows 4–6 m long).

The research team measured the following agro-morphological traits in the trials: days to 50% flowering (DF), plant height (PHT), disease and pest resistance, stay-green trait, panicle type (compact, semi-compact, loose), panicle number and panicle weight per plot, grain humidity at harvest stage and 1000-kernel weight (TKW).

The average grain weight of one panicle (GW1P) and grain yield (GRY) were calculated from the panicle weight per plot, applying a standard 0.80 coefficient (Paul, 1990), and were assessed at 14% moisture. Fodder yield and the leaf/stem ratio were measured for the 2007 CNIA trials only.

An “index of agronomic suitability” (IAS) was defined for combining four quantitative agronomic traits measured in the trials (DF, PHT, TKW and GRY), related to farmers’ preferences identified during the previous PVS work (Trouche et al., 2009). It was computed as following:



^a RS = rainy season = *postrera* season

^b DS = dry season (irrigated)

⁺ In the PCR-2 population, S₁s from BoF selection were planted on-farm during the 2006 rainy season but the material was lost because of drought

Fig. 1. History of the centralized (CNIA station) and decentralized (Totogalpa and Pueblo Nuevo) breeding schemes developed from the PCR-1 and PCR-2 populations.

Table 3
Plant number and selection intensity applied on-farm and on-station in the PCR-1 and PCR-2 populations.

Breeding population	PCR-1			PCR-2	
	BoS	FoF	BoF	BoS	FoF
Plant number in the S ₀ generation at maturity phase	1250	1500	1500	2400	2350
S ₁ plant-progenies selected	62	62	62	124	118
Selection intensity (%)	5	4	4	5	5
S ₂ plant-progenies selected	73	76	68	110	169

Index of agronomic suitability for the line *i*:

$$IAS_i = \sum_j a_j * \left[\frac{x_{ij} - m_j}{s_j} \right]$$

where x_{ij} is the phenotypic value of the line *i* for trait *j*, m_j the mean performance and s_j the standard deviation of all lines for trait *j*, a_j is the relative weighting of trait *j* in the index, where $j = 1-4$ (1 = DF; 2 = PHT; 3 = TKW; 4 = GRY).

In our study, a specific IAS was defined for each target ecosystem. The respective weightings of traits in each specific IAS were based on the preferred ideotypes by local farmers, mitigated with their agronomic value in their environment according to the breeder's experience.

Thus, the respective weightings for the four traits were defined as follow:

IASe (Tototalpa ecosystem): $a_1 = -3$; $a_2 = -2$; $a_3 = 3$ and $a_4 = 4$;
IASm (Pueblo Nuevo ecosystem): $a_1 = -2$; $a_2 = -4$; $a_3 = 2$ and $a_4 = 3$

2.6. Statistical analyses

To compare the phenotypic variability of the lines derived from the studied selection mode, a factorial discriminant analysis (FDA) was performed on a set of six and seven agro-morphological traits observed in the 2007 on-station yield trials, for the PCR-1 and PCR-2 lines respectively.

To analyse the grain yield stability of the different families of lines, we performed a standard regression analysis of the yield of individual lines over the trial mean, from the data for the common five PCR-1 and nine PCR-2 lines evaluated at both on-station on-farm locations from 2006 to 2008. These common lines represented the 20% top lines selected in the 2007 trials as explained earlier, after discarding lines showing germination problems or excessive heterogeneity in the 2008 evaluation.

ANOVAs were based on a fixed effects model and were performed with the SAS Statistical Software Package using the GLM procedure. FDA and regression analysis were performed using XLstat software version 2009 6.02.

3. Results

3.1. Phenotypic variability

The FDA did not display any significant difference between the selection modes for global phenotypic variance at the S₂ generation stage. As for single trait variability, they expressed significant differences for TKW in the PCR-1 population only, with BoF lines presenting higher variability than FoF and BoS lines (data not shown).

Analyzing the PCR-1 population, the centres of gravity which represents the average phenotype produced by each selection mode, clearly showed distinct coordinates (Fig. 2). Regarding both

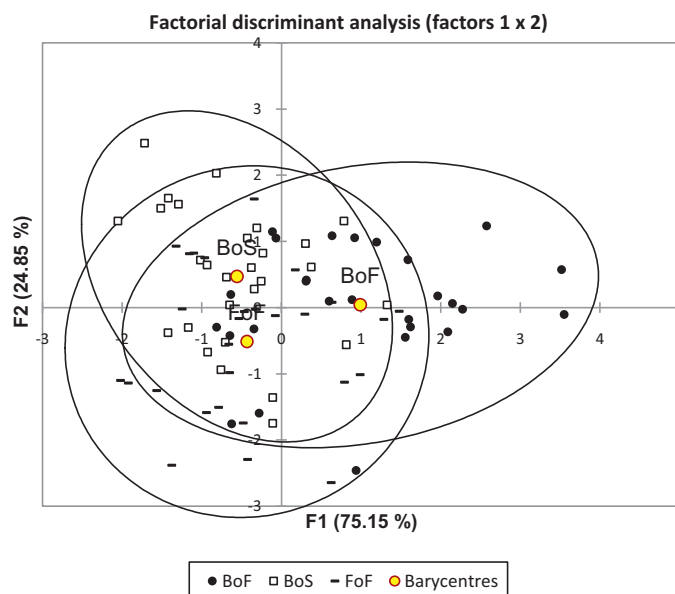


Fig. 2. FDA plot for 30 S₂₋₄ lines derived from the three selection modes applied to the PCR-1 population, characterized for six agro-morphological variables evaluated on-station in 2007.

populations, their position resulted from different selection pressures applied to individual single traits, i.e. DF, PHT, TKW and GW1P in PCR-1, DF and panicle type in PCR-2 (Table 4).

Moreover, we observed at the S₀ generation stage that there was an agreement between FoF and BoF in the selection of 15 plants (24% of total selected plants) and 52 plants (43%) for PCR-1 and PCR-2 respectively. Overall, FoF selection decreased phenotypic diversity as much as BoS selection, but it produced divergent "average phenotypes" especially marked for earliness.

3.2. Heritability of the agronomic traits measured in the on-station and on-farm trials

The ANOVA results for the on-station and on-farm trials in 2007 and 2008 revealed significant differences between genotypes for 81% of the traits in the harvested trials (data not shown). Table 5 presents the basic statistical parameters derived from the ANOVA for the four most important agronomic traits measured. In on-station and on-farm trials, the observed values of the coefficient of variation (CV) varied from good to fair; they were within the range of CVs commonly observed for sorghum trials under tropical conditions. The CV values of the on-farm trials were understand-

Table 4

Inter-mode divergences computed by the FDA for six and seven agro-morphological traits measured in the 2007 on-station trials on the S₂ lines derived from the PCR-1 and PCR-2 populations.

Population	Comparison	Inter-mode differences ^a	Traits contributing with significant differences between selection modes
PCR-1	Global (3 modes together)	**	DF, PHT, TKW and GW1P
	FoF vs. BoF	**	
	FoF vs. BoS	ns	
	BoS vs. BoF	**	
PCR-2	FoF vs. BoS	**	DF and panicle type

ns: non significant, * $P < 0.05$, ** $P < 0.01$.

^a Significance of Wilks' lambda likelihood ratio used to test the equality of the mean vectors of the selection modes in comparison.

Table 5
Coefficient of variation and heritability values of the traits measured in the trials evaluating the lines derived from the PCR-1 (S_{2-4} generation) and PCR-2 (S_{2-3} generation) populations, managed on-station and on-farm.

Population	Trait	Coefficient of variation (%)		h^2		
		On-station	On-farm ^a	On-station	On-farm ^a	On-farm mean for other yield trials in the target environment
PCR-1	DF	2.1	2.5 (2.4–2.6)	0.82	0.40 (0.18–0.63)	0.70
	PHT	6.4	9.1 (7.3–11.0)	0.85	0.56 (0.44–0.68)	0.52
	TKW	5.9	5.2 (2.7–7.6)	0.80	0.61 (0.31–0.91)	0.65
	GRY	13.2	25.1 (21.6–28.6)	0.57	0.19 (0.10–0.28)	0.21
PCR-2	DF	1.9	3.0 (2.5–3.5)	0.67	0.71 (0.63–0.78)	0.61
	PHT	6.2	7.6 (7.1–8.1)	0.73	0.59 (0.44–0.78)	0.62
	TKW	5.4	6.8 (3.9–9.8)	0.81	0.78 (0.69–0.87)	0.66
	GRY	14.6	20.2 (19.1–21.3)	0.47	0.31 (0.17–0.44)	0.36

DF, days from sowing to 50% flowering; PHT, plant height (m); TKW, 1000-kernel weight (g); GRY, grain yield ($t\ ha^{-1}$).

^a Mean value and range.

ably higher than those obtained on-station, the largest differences being observed for grain yield. The Totogalpa-2008 trial evaluating PCR-1 lines was discarded for lack of precision.

Broad sense heritability was high for all variables in the on-station trials, and especially for the simple traits DF, PHT and TKW as compared with GRY. Heritability values were less consistent on-farm. They were very close to those observed on-station for TKW, about 25% lower for DF and PHT, and only half for GRY. Heritability was particularly low at Totogalpa in 2007 and Palacagüina in 2008 for GRY, and at Pueblo Nuevo in 2008 for DF. In general, heritability estimates were higher in the PCR-2 trials compared with those assessing PCR-1 lines.

3.3. Simple traits

In both populations, FoF selection produced earlier and shorter lines with slightly heavier kernels than BoS selection did (Table 6). The difference in earliness was significant both on-station and on-farm for the two populations. Differences in plant height were only significant for PCR-2 population (on-farm data). Between these two modes, we did not observe significant difference in kernel weight. There was also no difference between BoS and FoF selection regarding fodder yield and leaf/stem ratio, two important traits for dual-purpose sorghum which was a priority of the PCR-2 population (data not shown). Compared to FoF selection, BoF selection in the PCR-1 population significantly reduced plant height and increased cycle duration, with no effect on kernel weight.

3.4. Grain yield

3.4.1. On-station yields

In both schemes, BoS lines persistently produced higher yields than FoF or BoF lines (Table 7). In the PCR-1 population, BoS lines

outyielded FoF lines by 6% and BoF lines by 17%. The difference was 5 and 10% respectively when comparing the top 20% lines of each mode. BoF selection was significantly less effective than BoS selection. BoS lines also outyielded FoF lines by 12% in the PCR-2 population, considering all lines or the 20% top yielding lines.

3.4.2. On-farm yields

Grain yields were high at Pueblo Nuevo in 2007 compared to the other on-farm sites because the experimental plot combined fertile soil, favourable rainfall, high planting densities and high fertilization decided by the local FB group. BoS lines globally outyielded FoF lines in both breeding schemes, although the advantage was somehow less consistent than we observed on-station (Table 8). In the PCR-1 population, BoS lines were not significantly better than FoF lines and there was no significant difference between BoF and FoF selection. In the PCR-2 population, BoS selection was more consistently better than FoF selection, although the difference was only significant for the 20% top-yielding lines at Pueblo Nuevo in 2007 (data not shown). In general, BoS selection for yield looked more efficient than FoF selection, when the lines were tested under favourable conditions, and at least equally efficient when they were tested under less favourable conditions.

3.4.3. Yield stability

On average, the regression coefficients of BoS lines were higher than FoF lines, though not significantly, while the main BoS lines showed regression coefficients above 1 (Table 9).

In the PCR-1 population, the average grain yield of the top five BoS lines ($3.56\ t\ ha^{-1}$) was 16% higher than the FoF lines ($3.08\ t\ ha^{-1}$) and 29% higher than the BoF lines ($2.75\ t\ ha^{-1}$). On average, BoS lines performed better than FoF and BoF lines in more favourable environments and also in less favourable to very low-yield environments (lower than $0.5\ t\ ha^{-1}$) (Fig. 3). We did not observe cross-over interaction between the three selection modes

Table 6
Performance of lines derived from PCR-1 (S_{2-4} generation) and PCR-2 (S_{2-3} generation) for simple traits depending on the selection mode (station and on-farm trials, 2007).

Population	Treatment	CNIA station (2007)			On-farm environment (2007)		
		DF	PHT	TKW	DF	PHT	TKW
PCR-1	FoF	59.6	1.96	29.8	64.3	1.52	28.3
	BoS	61.9	2.06	29.8	65.6	1.56	27.8
	BoF	61.7	1.69	27.3	66.5	1.35	27.8
	Isd (5%)	1.37	0.13	1.99	1.18	8.31	1.49
	Check ^a	61.5	2.25	35.3	64.6	1.65	31.6
PCR-2	FoF	62.6	1.93	32.0	63.7	1.86	32.3
	BoS	63.7	1.99	31.0	65.4	1.96	31.1
	Isd (5%)	0.66	0.08	1.33	1.11	0.07	1.26
	Check ^a	65.1	1.74	29.0	70.4	1.65	28.5

DF, days to 50% flowering; PHT, plant height (m); TKW, 1000-kernel weight (g); FoF, farmers on-farm; BoS, breeder on-station; BoF, breeder on-farm.

^a Blanco Tortillero for PCR-1 and MACIA for PCR-2.

Table 7Grain yield (t ha^{-1}) of the S_2 lines derived from the PCR-1 and PCR-2 populations depending on the selection mode (on-station trials, 2007–2008).

Treatment	Grain yield (t ha^{-1})			
	PCR-1		PCR-2	
	CNIA-07 all ($n=28$)	CNIA-07 20% top ($n=6$)	CNIA-07 all ($n=60$)	CNIA-07 20% top ($n=12$)
FoF	5.08	6.19	4.87	5.92
BoS	5.41	6.48	5.44	6.61
BoF	4.62	5.91	–	–
<i>lsd</i> (5%)	0.47	0.22	0.31	0.30
Check ^a	6.22	6.22	5.20	5.20

n: number of lines compared for each selection mode.

FoF, farmers on-farm; BoS, breeder on-station; BoF, breeder on-farm.

(–) The lines were not evaluated.

^a Blanco Tortillero for PCR-1 and MACIA for PCR-2.**Table 8**Grain yield (t ha^{-1}) of the S_2 lines derived from the PCR-1 and PCR-2 populations depending on the selection mode (on-farm trials, 2007–2008).

Treatment	Grain yield (t ha^{-1})						
	PCR-1			PCR-2			
	Totogalpa-07 ($n=28$)	CECOOP-08 ($n=5$)	Mean	Pueblo Nuevo-07 ($n=60$)	Unile-08 ($n=11$)	Palacagüina-08 ($n=11$)	Mean
FoF	1.98	1.23	1.63	4.36	1.53	2.35	2.75
BoS	1.95	1.64	1.79	4.64	1.86	2.41	2.97
BoF	1.79	1.24	1.53	–	–	–	–
<i>lsd</i> (5%)	0.15	0.59	0.29	0.29	0.38	0.39	0.29
Check ^a	1.85	1.70	1.78	3.08	1.61	1.81	2.17

n: number of lines compared for each selection mode.

FoF, farmers on-farm; BoS, breeder on-station; BoF, breeder on-farm.

(–) The lines were not evaluated.

^a Blanco Tortillero for PCR-1 and MACIA for PCR-2.

in the range of the tested environments. However, as regards the performance of individual lines, FoF selection succeeded in providing the best yielding (and more stable) line in the range of 1–3 t ha^{-1} .

In the PCR-2 population, the average grain yield of the top nine BoS lines (4.04 t ha^{-1}) was also 17% higher than the FoF lines (3.46 t ha^{-1}). On average, BoS lines showed higher yield than FoF lines in favourable and intermediate environments. Cross-over interaction between two modes was observed at 1.1 t ha^{-1} (Fig. 3).

3.5. Agronomic suitability

In both schemes, the FoF lines globally achieved better IAS values (Table 10). The only exception concerned the results of CECOOP-08 for the PCR-1 lines. The superiority of FoF selection was more obvious in the case of the 20% top-IAS lines in the 2007 trials, which included a larger number of lines. FoF selection gave better results with the PCR-2 population than the PCR-1 population (based on the comparison of gains with BoS as well as the control varieties). The performance of the BoF lines was poorer than that of the FoF and BoS lines.

Table 9

Yield stability over environments of the lines derived from the PCR-1 and PCR-2 populations depending on the selection mode, measured by average value for regression coefficient and proportion of lines with regression coefficient above 1.

Selection mode	Average <i>b</i> value		$b > 1^a$	
	PCR-1 lines	PCR-2 lines	PCR-1 lines	PCR-2 lines
	FoF	0.997 a ⁺	0.889 a	3/5
BoS	1.124 a	1.113 a	4/5	6/9
BoF	0.880 a		1/5	

^a Proportion of selected lines with $b > 1$.⁺ Means with the same letter are not significant different at $p = 0.05$ (Tukey test).

4. Discussion

4.1. Phenotypic variability

For both breeding schemes considered in this study, FoF selection carried out on-farm at on-site reduced the initial phenotypic variability as much as BoS selection. In a PPB work on cotton in Benin, Lançon et al. (2008) had shown the effectiveness of FoF selection in decreasing the genetic variability of a segregating population. However, in an earlier paper based on selection theory, Witcombe et al. (1996) predicted that PPB would better maintain or even increase genetic diversity under most circumstances. However, more recent field studies supported our results. Virk and Witcombe (2007) did not find that the rice cultivars A228 (derived from consultative PPB) and A200F (derived from collaborative PPB) conserved more intra-variety genetic diversity than varieties derived from conventional breeding. Analysing the effect of one cycle of selection, Fufa et al. (2007) concluded that there was no difference in allelic frequencies found in heterogeneous populations of barley bred by either farmers or breeders at six locations. In our work, the groups of FBs involved were fairly uniform and this limited the possibility of divergent selection between the farmers. In fact, the farmers were representatives of a broader target group farming in a small region, the size of a “municipio”, with fairly similar cropping systems. For some traits, BoF selection maintained greater phenotypic diversity between the lines produced than BoS and FoF. We predicted that BoF was less able than FoF to provide consistent selection under poor conditions, low soil fertility and heterogeneous plots.

4.2. Gains in simple traits

Despite the use of common breeding goals and criteria, FoF and BoS selection ended up with different average phenotypes. In particular, FBs tended to select earlier materials than the breeder

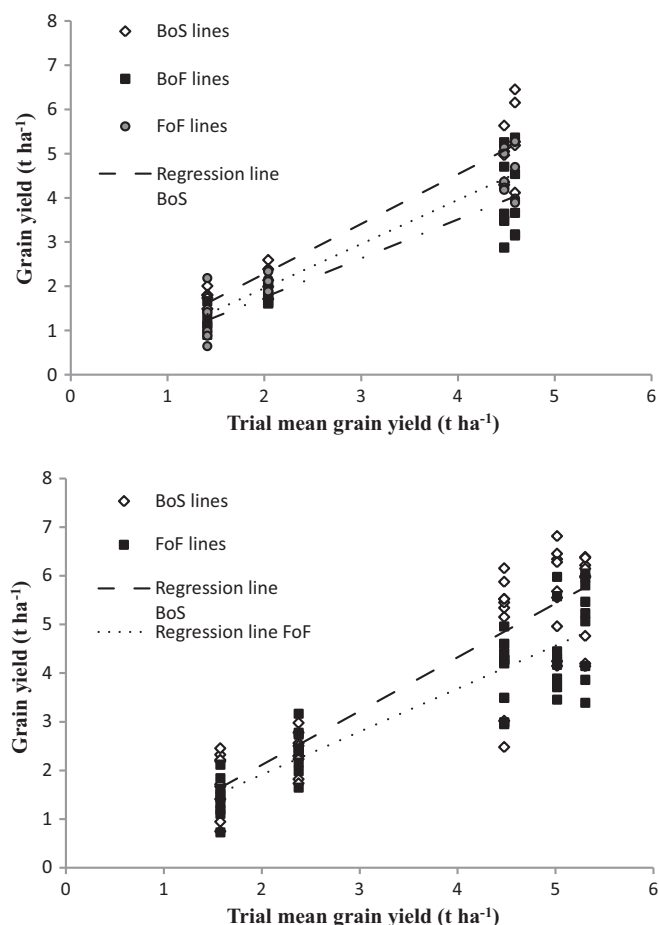


Fig. 3. Grain yield ($t\ ha^{-1}$) of individual lines at various yield levels indicated by trial means. Top: 15 PCR-1 lines tested in four on-station and on-farm environments (2006–2008). Down: 18 PCR-2 lines, tested in five on-station and on-farm environments (2007–2008).

did on-station and on-farm. Several studies showed that earliness could easily be assessed by farmers (Joshi and Witcombe, 1996; Mutatu and Zelleke, 2002; Trouche et al., 2009). As PCR-1 was targeted for the driest areas, an intense focus of FBs in favour of earliness was in line with the priorities defined initially as well as the farmers' preferences expressed during the PVS phase in this region (Trouche et al., 2009). Similar inclinations were highlighted in other farmers' breeding work implemented in drought-prone environments (Virk et al., 2003; vom Brocke et al., 2010). However, regarding the PCR-2 population, the FBs' focus on earliness was not fully in line with previously defined breeding goals and actual climatic need. Excessive focus of farmers on earliness is a frequent

bias observed in participatory breeding as already stated in various papers (Lançon et al., 2006; Sissoko et al., 2008). Often, choosing a date for a collective evaluation needs a compromise between participants' agendas: at the end, farmers can only evaluate what they see when the exercise takes place. In our experience, evaluation was generally performed before the breeding materials were fully mature. The FBs explained that they selected mature early plants, because yield and grain appearance were already settled and guaranteed at that time. They preferred not to take a bet that later varieties would have greater yield potential with adequate grain quality. On the other hand, the breeder was less attentive to earliness for at least two reasons. First, the breeder has a more in-depth and general experience of the crop and he can better predict the potential of sorghum lines at various stages. Also, he has many opportunities, especially on station, for assessing the breeding materials at the most relevant periods of their development.

In addition, our study highlighted that FoF selection was effective for decreasing plant height and, to some degree, increasing kernel size. As shown before, these two traits are highly heritable and their expression is thus little affected by on-farm conditions. In general, farmers prefer a reduced plant height that makes manual cutting of panicles easier. Where fodder use is given a high priority, as in Pueblo Nuevo area, farmers consider that shorter plants, with a high proportion of green leaves at maturity, provide fodder of higher quality.

4.3. Gains in grain yield: response to selection

The selection theory (ST) model proposed by Falconer (1989) and adapted by Bänziger and Cooper (2001) could be used as a guideline to understand the yield results observed in this study. It proposes to compute the response to selection R_T as the product between the genetic variance of the population under selection (σ_G^2), selection intensity (i), heritability in the selection environment (H_{se}^2) and the genetic correlation between selection and target environments (r_G).

In our study, the selection intensity and genetic variance were common to the three selection modes and both populations. According to the ST model, differences in responses to selection could only be attributed to differences in H_{se}^2 or r_G . As far as heritability for yield was concerned, our data indicated that it was low in the Totogalpa environment (PCR-1), intermediate in the Pueblo Nuevo environment (PCR-2) and high in the CNIA station environment. The r_G coefficient is expected to be high (close to 1) when selection and target environment are very similar and low when the two environments display large differences (considering soil fertility, climatic constraints and input levels). In our study, the r_G between on-station and on-farm environments were thus expected to be lower for the Totogalpa target environment than for the Pueblo Nuevo environment.

Table 10

IAS index of the S_2 lines derived from the PCR-1 and PCR-2 populations depending on the selection mode (on-farm trials, 2007–2008).

Treatment	Index of agronomic suitability IAS						
	PCR-1			PCR-2			
	Totogalpa-07: top 20% (n=6)	CECOOP-08 (n=5)	Mean	Pueblo Nuevo-07: top 20% (n=12)	Unile-08 (n=11)	Palacagüina-08 (n=11)	Mean
FoF	10.19	0.31	5.25	7.37	0.26	2.66	3.43
BoS	7.91	3.01	5.46	5.04	-0.92	-1.60	0.84
BoF	6.97	-1.98	2.50	-	-	-	-
<i>l</i> sd (5%)	3.08	5.75		0.58	3.42	4.72	
Check ^a	2.69	6.20	4.45	-4.20	-0.89	4.17	-0.31

n: number of lines compared for each selection mode.

FoF, farmers on-farm; BoS, breeder on-station; BoF, breeder on-farm.

(-) The lines were not evaluated.

^a Blanco Tortillero for PCR-1 and MACIA for PCR-2.

In comparison with the model, our results, which denoted a fairly consistent superiority of BoS over FoF selection for yield, showed that heritability values were highly critical in determining R_T and the r_G value between the on-station and Totogalpa environments was not as low as expected, notwithstanding the environmental differences between sites. Rationally, the calculation of narrow sense heritability values for yield in each selection environment would have provided more accurate results in predicting response to selection. Unfortunately, our study did not allow us to make these calculations. Moreover our experience let us believe that the relative importance of additive genetic variance in the total genetic variance should not be biased by the selection environment or who made the selection, thus we think that our conclusions remain valid.

This observation does not question the ability of farmers to visually identify high-yielding genotypes in stressful environments. On-farm selection for yield could probably be more advantageous when target and station environments were drastically different, as shown in participatory breeding on barley by Ceccarelli et al. (2000) or on rice by Sthapit et al. (1996).

4.4. Yield stability

Our data showed that FoF selection produced lines with globally better yield stability than those developed by BoS selection. This was in agreement with theory (Simmonds, 1991) as well as some experimental results (Ceccarelli et al., 2003; Virk et al., 2003).

In both the PCR-1 and PCR-2 populations, there was a cross-over interaction between BoS and FoF lines, showing that lines derived from FoF selection were more productive at low yield levels and less productive at high yield levels. However, for the PCR-2 lines, the cross-over point was equivalent to about 1 t ha^{-1} , which was in range with the usual yields obtained by farmers in their own fields ($0.7\text{--}2.2 \text{ t ha}^{-1}$), while it was much lower for the PCR-1 lines. In both cases, BoS selection produced higher-yielding lines, but their superiority decreased in unfavourable environments. This reminds us that breeding for productivity can be effectively conducted on-station, as long as the essential yield components for the target environment are properly expressed. Sthapit et al. (1996) reported a case in Nepal where this minimum requirement was not met. As the main station for rice breeding is situated at a low elevation, where no cold constraint exists, the conditions were too distant from the target crop environment of the highlands to be effective for breeding. To develop suitable varieties for this highland environment, breeders decided to implement an *in situ* participatory selection programme instead of opening a new station at a higher elevation.

4.5. Gains in appropriate combination of traits

Based on the IAS index, FoF selection produced a larger number of lines with a good balance between earliness, grain yield and grain size in the PCR-1 population, and between plant height and grain yield in the PCR-2 population, comparing to BoS selection. We can consider that FoF maintained the selection priorities they had initially fixed, despite some bias, such as an excessive focus on earliness in PCR-2. BoS selection tended to be more focused on grain yield and more lenient with plant height or grain size. This is in phase with the results of other studies. Gyawali et al. (2007) reported that farmers' selection lead to a superior combination of yield and earliness on rice in Nepal. In other cases, farmers' selection achieves superior combination of yield and grain quality for the market on bean in Colombia and Costa Rica (Kornegay et al., 1996; Araya-Villalobos and Hernández-Fonseca, 2006). In fact, farmers generally look for good yield in well-defined phenotypes in combi-

nation with eliminatory quality traits, as underlined by Atlin et al. (2001).

BoF selection in PCR-1 was no more successful for the IAS index than it was for yield. We think that the formal breeder was not prepared to select plants in heterogeneous plots and low-fertility soils (as occurred in the PCR-1 on-farm breeding plots). In an unfamiliar environment, a breeder cannot fully reconstruct the history of a plant and properly evaluate its genetic potential. In our case, the breeder unintentionally placed the emphasis on low plant height at the expense of productivity, because of the over-selection of short but weak plants with nice grains identified under the low-fertility soil conditions, while in this area this criterion was not so important for farmers (low weighting in the IAS index).

5. Conclusion

The main three results of these two PPB programmes on sorghum in Nicaragua could be summarized as follows:

- After two selection cycles, the selection made on-farm by farmer-breeders reduced phenotypic variability as much as the selection carried out on-station by the breeder.
- Overall, BoS selection produced lines with better yield potential even in the target environment.
- FoF selection produced more balanced genotypes, with a combination of earliness, plant height, grain size and yield closer to what was expected by farmers for coping with the local constraints.

In addition, under heterogeneous and highly restrictive conditions, BoF selection did not prove to be as effective as FoF selection, for either yield or for the IAS index.

Three lessons can be drawn from this study. Firstly, our results support the idea that a professional breeder can do a good job on-station as long as he cares understanding the constraints of target cropping systems and farmers' objectives, in order to accurately identify the resulting breeding goals and selection criteria. Secondly, we have to bear in mind that breeding on-farm faces several limitations. The participants had little control over two of those limitations, perhaps the most acute: (i) in semi-arid areas, very strong inter-annual rainfall variability may affect the accuracy or even relevance of plant selection and (ii) for complex traits such as yield, heritability is particularly low in farmers' fields. On the other hand, the study also highlighted that FBs cannot always devote enough time to this selection activity, and that the period for assessing the genetic material was fixed by compromise, what could bias its evaluation. In ideal conditions, this should be improved by a touch of FB professionalization conducive to greater autonomy for planning and managing evaluation and selection activities. Lastly, FBs may face problems in handling large segregating populations. In particular, we observed that the S_1 generation, which included a great number of progenies with high intra and inter-genetic variability, has been difficult to manage on-farm, and difficult to assess for farmers. Probably it would be more efficient if this phase was managed on-station by a professional breeder.

These limitations and the lessons we drew from them all tend to support the need of closer and more interactive collaborations between farmers and breeders. Looking for complementarities and continuous dialogue could be the best insurance for developing varieties better adapted to stress and/or specific production systems and more accepted by farmers.

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