

Can Tall Guinea-Race Sorghum Hybrids Deliver Yield Advantage to Smallholder Farmers in West and Central Africa?

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ABSTRACT

Many farmers in West and Central Africa (WCA) prefer tall (>3 m) grain sorghum [*Sorghum bicolor* (L.) Moench] for various reasons. This study seeks to determine (i) what yield superiority newly bred, tall, photoperiod-sensitive guinea-race sorghum hybrids can provide relative to an adapted landrace variety across a wide range of productivity conditions, and (ii) the risk of these hybrids failing to provide yield superiority for individual farmers. Seven hybrids, one local check, and eight pure-line progenies were evaluated in 37 farmer-managed, on-farm yield trials across three Malian zones and 3 yr. Environments were classified into four productivity groups (low [0.78–1.10 Mg ha⁻¹], mid-low [1.10–1.50 Mg ha⁻¹], mid-high [1.50–2.00 Mg ha⁻¹] and high [2.00–2.65 Mg ha⁻¹]) based on their trial mean grain yield. Mean yields of the seven tall hybrids were 3 to 17% (ranging from 0.06 to 0.28 Mg ha⁻¹) higher than that of the local check across all environments and were highest (14–47%) averaged across the seven trials with the lowest mean yields. The individual overall highest-yielding hybrid showed superiorities over the local check in the low, mid-low, mid-high, and high productivity levels of 0.43 (47%), 0.14 (10%), 0.47 (27%), and 0.34 (14%) Mg ha⁻¹, respectively. The tall hybrids rarely had yields significantly inferior to the local check. Farmers' preference for, and the possible benefits of, taller plant types may lead farmers to grow tall hybrids, particularly under the typical low-productivity production conditions of WCA.

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Abbreviations: AMMI, additive main effect and multiplicative interaction; EM, expectation maximization; GEI, genotype-by-environment interaction; ICRISAT, International Crops Research Institute for the Semi-Arid Tropics; IER, Institut d'Economie Rurale; IPC, interaction principal component; Kp, photoperiod sensitivity index; PLEC, pure-line experimental cultivars; WCA, West and Central Africa.

SORGHUM BICOLOR (L.) MOENCH is a major staple cereal crop in the savannah zone of West and Central Africa (WCA) that is typically grown under low-input conditions. Soil fertility levels are generally low in these cropping systems (Jones and Wild, 1975; Bationo et al., 2007). With population growth contributing to rising demand, the area of sorghum production is steadily increasing (FAOSTAT, 2015), yet sorghum productivity has not increased substantially during the past 50 yr; the long-term sorghum grain yield in WCA averages approximately 1 Mg ha⁻¹ (Chantereau et al., 2013; FAOSTAT, 2015).

The guinea race, one of the five major sorghum races (Harlan and de Wet, 1972), being vital for food security in the Sudanian and Northern Guinea zones of Senegal, Mali, and Burkina Faso, is extensively cultivated in WCA (de Wet and Huckabay, 1967). The guinea race has the broadest geographical distribution

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(de Wet et al., 1972; Harlan and de Wet, 1972) and greatest genetic diversity of the major sorghum races (Folkertsma et al., 2005; Billot et al., 2013). This race, domesticated in WCA (Dahlberg, 2000), has hard grains of symmetrical form that twist relative to widely opening glumes at maturity in lax panicles.

Despite the creation of new shorter-statured varieties, many farmers still grow landrace varieties that are tall (>3 m) and photoperiod sensitive (Kimber et al., 2013). The photoperiod sensitivity and taller plant height reduce grain-mold damage and bird predation by enabling optimal timing of grain filling near the end of the rainy season, better shedding of rain water, and hindering birds from roosting on the swaying, drooping, lax panicles born on long peduncles. Further, the taller height can aid in competition with weeds and reduce risks of panicle loss by grazing transhumant cattle.

Sorghum hybrid breeding began in 1927 (Conner, 1927), but commercial hybrids were feasible only after the identification of a heritable and stable cytoplasmic male sterility (CMS) mechanism (Stephens and Holland, 1954). Sorghum hybrids have shown potential to outyield their parents and local varieties under drought conditions in Eastern Africa (Blum et al., 1992; Haussmann et al., 1997, 1998, 1999, 2000). Hybrid crosses of Malian landraces with introduced caudatum-race seed parents showed good heterosis for grain yield, but they lacked the grain quality required for production in the guinea-race zone of WCA (Touré and Scheuring, 1982). These results, and farmers' demand for higher-yielding varieties, motivated the Institut d'Economie Rurale (IER) and the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) in Mali to test the feasibility of breeding hybrids based on photoperiod-sensitive, guinea-race germplasm (Smale et al., 2014; Weltzien, 2014). The shorter (<3 m) hybrids from the first series of guinea-race hybrids combined good grain quality with grain yield superiorities of up to 37% over the highly appreciated guinea landrace variety 'Tieble' under farmers' field conditions (Rattunde et al., 2013).

Therefore, the objectives of this study were (i) to determine the yield performance of tall photoperiod-sensitive sorghum hybrids relative to farmers' adapted landrace varieties under a range of Malian farmers' production conditions and (ii) to understand what, if any, risk these new tall hybrids may pose for not recovering the farmer's investment in purchased hybrid seed through sufficient yield superiorities.

MATERIALS AND METHODS

Genotypes

Based on grain yield and plant height data from trials at the IER and ICRISAT research stations near Bamako, Mali, in 2007 and 2008, seven tall sorghum hybrids (>3 m) were identified for farmer-participatory testing out of a set of 55 hybrids. The

seven hybrids in this study were produced using two A1 cytoplasmic male-sterile seed parents, either the tall FambeA or the shorter (intermediate stem internode length) GP271A (Supplemental Table S1). The maintainer line for FambeA was derived from a mutagenized Malian guinea landrace variety, and that for GP271A was derived from an ICRISAT-IER random-mating population based on guinea landrace germplasm (Rattunde et al., 1997). The male parents consisted of four restorer lines derived from tall guinea landrace varieties (IS2731 from Burkina Faso, CSM388 and CSM63E from Mali, and Zabuwa from Nigeria) and two breeding lines with intermediate stem internode lengths (Lata, derived from a random-mating guinea-race population, and CGM 19/9-1-1 from a biparental guinea-race cross).

The eight pure-line experimental cultivars (PLEC) included in the farmer participatory yield trials were derived by IER in the F₅ generation from interracial guinea-caudatum material. They were identified on the basis of high yields in initial yield trials conducted at IER research stations (Cinzana, Bema, Sotuba, and Kolombada).

The tall landrace cultivar Tieble (CSM335 from the Malian Collection), highly appreciated by farmers for its yield stability and good grain quality, was included in the trial as a local check variety. One hybrid (Wagui) was dropped after the first-year (2009) trials because it was clearly rejected by farmers on account of its late maturity. This hybrid was replaced by a second, slightly late-maturing Malian landrace, Doua-G, for the second- (2010) and third-year (2011) trials.

Participatory On-Farm Yield Trials

Thirty-seven on-farm yield trials were conducted in three of the major sorghum production zones of Mali: the Dioila and Koutiala zones with more intensified agriculture and strong history of cotton (*Gossypium hirsutum* L.) production, and the Mandé zone with less intensified agriculture. The on-farm yield trials were conducted in three villages per zone (four villages in Dioila 2009), with two farmers chosen per village across two consecutive years (2009–2010 for Dioila and Mandé, and 2010–2011 for Koutiala) (Table 1), involving a total of 26 participating farmers as part of an ongoing participatory sorghum cultivar-testing program (Weltzien et al., 2008).

An α -lattice design, with two replications and four blocks of four plots per replication, was used for all on-farm trials. Plots consisted of six rows of 5-m length, with approximately 75 cm between rows and 40 cm between hills. Plots were sown with six seeds per hill, and hills were finally thinned to two plants around 4 wk after sowing. Sowing, weeding, thinning, and fertilization were conducted by the farmers. Sufficient fertilizer and calibrated measuring cups were provided to the farmers for manual application of 100 kg ha⁻¹ of diammonium phosphate and 50 kg ha⁻¹ of urea, which were generally applied after the first and second weedings, respectively.

Additional field trials were sown at the ICRISAT-Mali research station in the same field on 15 July 2009 and 26 June 2010 using an α -lattice design with four replicates. Plant heights and dates of 50% anthesis were recorded, and a photoperiod-sensitivity index (Kp) was computed using the following equation:

$$Kp = (DurF1 - DurF2)/(DS2 - DS1) \quad [1]$$

Table 1. Number of on-farm trials (N trials), sowing date ranges, precipitation (PPT), and mean grain yield by zone and by year

Zones	Mande		Dioila		Koutiala	
Year	2009	2010	2009	2010	2010	2011
N trials	6	6	8	6	6	5
Sowing dates	8–27 July	28 June–14 July	9–19 July	15–30 June	14–28 June	23 June–15 July
Total PPT (mm)	821	932	742	1088	1279	826
August PPT (mm)	223	214	167	350	325	175
Yield (Mg ha ⁻¹)	1.43	1.43	1.83	1.46	1.47	1.94

where DurF1 and DurF2 are the duration in days from sowing to 50% anthesis in the 26 June and 15 July sowings, respectively, and DS1 and DS2 are the first and second sowing dates in Julian days (Clerget and Rattunde, 2007). The value of Kp is expected to vary from zero, for photoperiod-insensitive cultivars that do not change the duration of their vegetative phase, to one, for the most strongly photoperiod-sensitive cultivars that reduce their vegetative phase to the same extent as the delay in sowing (19 d, in this case).

Statistical Analysis

Each farmer's trial in a given year was considered a separate environment. A mixed-model analysis using restricted maximum likelihood (REML) was conducted with the software GenStat, 17th edition (VSN International, 2014) to analyze the phenotypic data from the 37 on-farm environments across 3 yr. Single-environment data were first analyzed separately, treating replications as fixed and blocks nested within replications and genotypes as random. Repeatability (broad-sense heritability of single trials) estimates for each trial were based on an ad hoc approach for unbalanced datasets using formula 19 in Piepho and Möhring (2007). The average variance of differences among genotypes and the best linear unbiased estimates (BLUEs) of each genotype in each environment were obtained from a second model where genotypes were considered a fixed factor. Least significant differences (LSD, $\alpha = 5\%$) per environment were computed to compare genotypic means.

Environments were classified into four groups (low [0.78–1.10 Mg ha⁻¹], mid-low [1.10–1.50 Mg ha⁻¹], mid-high [1.50–2.00 Mg ha⁻¹], and high [2.00–2.65 Mg ha⁻¹]) based on their trial mean grain yield. A combined analysis of grain yield across all on-farm trials was done using a hierarchical model, treating all factors as random. Two separate multi-environment combined analyses were conducted, modeling a heterogeneous error term to account for the variable yield and error levels among environments. In the first analysis, we used a hierarchical model (Eq. [2]) with replications nested within environments and incomplete blocks nested within replications. From this model, we obtained the reference variance components, particularly for the genotype-by-environment interaction (GEI), the best linear unbiased predictors (BLUPs) for the genotypes, and an estimate of broad-sense heritability across all environments using formula 20 of Piepho and Möhring (2007). In the second analysis (Eq. [3]), we added environmental variables, one at a time, to examine the contributions of agroecological zone (Mande, Dioila, and Koutiala), yield level (four levels), or year to GEI (Leiser et al., 2012).

$$Y_{ijkl} = \mu + G_i + E_j + GE_{ij} + E(R)_{jk} + E[R(B)]_{jkl} + \varepsilon_{ijkl} \quad [2]$$

$$Y_{ijkl} = \mu + G_i + E_j + GE_{ij} + GF_{im} + E(R)_{jk} + E[R(B)]_{jkl} + \varepsilon_{ijkl} \quad [3]$$

where Y_{ijkl} is the observed yield value with the i th genotype in the l th incomplete block within the k th replication of the j th environment, G_i is the effect of the i th genotype, E_j the effect of the j th environment, R_k is the effect of the k th replication and B_l the effect of the l th block within the k th replication in the j th environment. Y_{ijkl} is the observed yield value of the i th genotype in the l th incomplete block within the k th replication of the j th environment and the m th environmental factor level. GF_{im} denotes the interaction effect of the i th genotype with the m th environmental factor (e.g., zone, year, and yield level). GE_{ij} denotes the interaction effect of the i th genotype with the j th environment. ε_{ijkl} and ε_{ijmkl} are the residual terms of the respective model.

The additive main effect and multiplicative interaction (AMMI) analysis and biplot (Gauch and Zobel, 1988; Gauch, 2013) were computed with the agricolae package (de Mendiburu, 2009) under the R software (R Development Core Team, 2011). Prior to the AMMI analysis, missing data were imputed, applying the expectation maximization (EM) algorithm (Gauch and Zobel, 1990) with the EM.AMMI function (Paderewski, 2013) in R. The genotypes Wagui (hybrid) and DouaG (local variety) were removed from the analysis because they were not present across all years and therefore would have a strong dependency on the imputation algorithm.

Yield stability of hybrids and Tieble across all environments was assessed by regressing the single-environment yields of each genotype against the respective environmental mean yields (Finlay and Wilkinson, 1963; Lin et al., 1986; Becker and Leon, 1988). The analysis was done using the Finlay and Wilkinson analysis tool implemented under Genstat 18th edition (VSN International, 2015).

RESULTS

Individual On-Farm Trials and Repeatabilities

Mean grain yields of the 37 on-farm trials varied from 0.78 to 2.60 Mg ha⁻¹ and genotypic mean yields within environments ranged from 0.37 to 3.74 Mg ha⁻¹. Although the trials were sown across a 6-wk period, between 14 June and 27 July, no relationship was observed between sowing date and trial mean grain yield ($r = 0.11$, $p = 0.53$, $n = 37$). Repeatability estimates for grain yield varied between 0.13 and 0.90 (median = 0.78) for individual trials, with only one having a repeatability below 0.57 (Supplemental Fig. S1, Supplemental Table S2), and had no significant relationship with mean grain yield ($r = 0.23$, $p = 0.18$, $n = 36$).

Genetic Differences and Genotype-by-Environment Interaction

Although the GEI was significant, the significant genotypic variance component was more than double the GEI variance component (Table 2). Inclusion of specific environmental factors to account for geographic zones, years, or productivity levels in the combined analysis reduced the GEI variance by only 11.7, 7.4, and 8.7%, respectively, relative to the original GEI variance; hence, these factors did not substantially explain the GEI variance. The broad-sense heritability estimate was 0.91, and combined analysis within each zone revealed significant GEI interaction only within the Dioila zone (Supplemental Table S3).

The AMMI analysis explained 28.6 and 19.4% of GEI with the first and second interaction principal components (IPC1 and IPC2), respectively, with no detection of clearly distinct mega-environments (Fig. 1). The hybrids (entries 9–14) exhibited greater GEI than PLECs, with the GEI of hybrids over the higher productivity environments being markedly greater than over the lower-yielding environments (Fig. 1, further hierarchical combined analysis [data not shown]). The PLECs (entries 1–8) and the local check Tieble (entry 16) had little to no interactive behavior, as indicated by their small to near-zero IPC1 and IPC2 scores. The two highest-yielding hybrids, Pablo (entry 9) and Caufa (entry 13), had the highest interactive behavior, displaying the largest yield ranges across environments, with minimums of 0.95 and 0.72 and maximums of 3.47 and 3.69 Mg ha⁻¹, respectively, across single environments.

Hybrid Performance Relative to the Local Check

The mean grain yields of the experimental hybrids ranged from 1.70 to 1.92 Mg ha⁻¹, which represented yields of 0.06 to 0.28 Mg ha⁻¹ (3–17%) higher than that of the local check Tieble, averaged across all 37 yield trials (Table 3). The hybrids, as a group, exhibited grain yields that were numerically higher than that of Tieble in the lower- and higher-yielding conditions (Table 4). However, only in the lowest productivity level was the hybrid mean significantly superior to Tieble's mean yield, with both the absolute and percentage mean yield advantage of hybrids being greater than in the higher-productivity levels (Table 4). The hybrid with the overall highest yield, Pablo, had a 0.43-Mg ha⁻¹ average yield superiority (47%) over Tieble in the lowest productivity trials and only a 0.34-Mg ha⁻¹ superiority (14%) in the highest productivity trials (Table 4).

Although there were cases of hybrids yielding less than Tieble in individual trials (Fig. 2), the frequency of significantly inferior yield was below 5% in all productivity levels, except mid-high, where it was 7% (Table 4). Out of 230 pairwise yield comparisons between Tieble and individual hybrids across all trials, in only nine comparisons did Tieble significantly (LSD, $\alpha = 5\%$) outperform a hybrid.

Table 2. Estimates of variance components (\pm SE) for genotypic (σ^2_g), environmental (σ^2_e), and genotype-by-environment interaction (σ^2_{ge}) sources of variance for sorghum grain yield over 37 on-farm trials and for the residual genotype-by-environment interaction (GEI) variance components after accounting for zone, year, and yield group.

Term	Variance component (\pm SE) [†]
σ^2_g	4.72** (\pm 1.75)
σ^2_e	20.46*** (\pm 5.17)
σ^2_{ge}	2.21*** (\pm 0.46)
Residual GEI variance (\pm SE) after accounting for:	
Zone	1.95*** (\pm 0.44)
Year	2.05*** (\pm 0.46)
Yield group	2.02*** (\pm 0.45)

** Significant at the 0.01 probability level.

*** Significant at the 0.001 probability level.

[†] Variance components were multiplied by 100 for better readability.

Individual hybrids had significantly higher yield than Tieble in 42 cases, with Pablo (11) and Caufa (9) accounting for half of these cases. Whereas the hybrids exhibited significant superiority to Tieble in 31% of the comparisons among the seven lowest-yielding trials, among the eight highest-yielding trials, they did so in only 17% of the pairwise comparisons. The hybrids Pablo and Wagui were among the top four hybrids that outperformed Tieble across all four yield groups (Supplemental Table S4).

Based on the linear regression analysis (Supplemental Fig. S2), Pablo (slope $b = 1.21$) and Tieble ($b = 1.12$) had

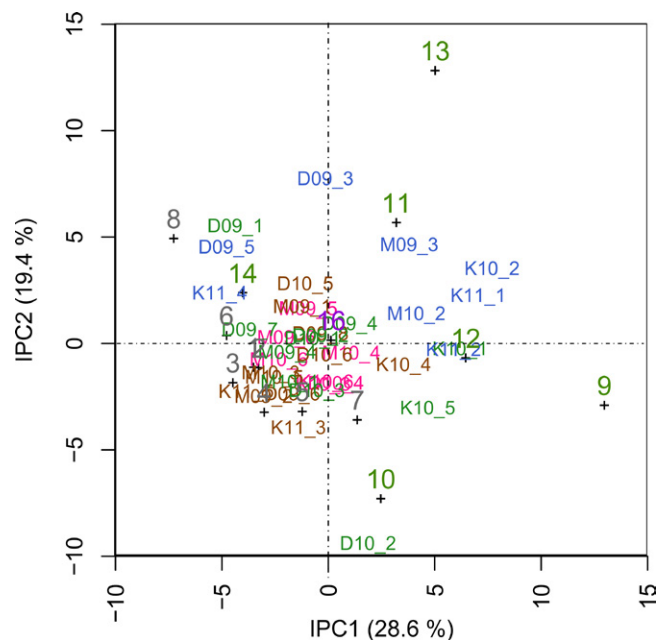


Fig. 1. Additive main effect and multiplicative interaction (AMMI) 2 biplot of 15 Guinea sorghum cultivars (hybrids in green, local check in violet, and pure-line experimental cultivars [PLECs] in grey) tested in 37 on-farm trials in Mali between 2009 and 2011. The environments in low-, mid-low-, mid-high-, and high-yielding environments are respectively in pink, brown, green, and blue. Entry numbers and codes for environments are described in Table 3 and in Supplemental Table S2, respectively.

Table 3. Grain yields (Mg ha⁻¹) and plant height (cm) best linear unbiased predictors (BLUPs) of 17 sorghum cultivars over 37 on-farm trials and the absolute value and difference of each cultivar's grain yield relative to 'Tieble', as well as their dates of 50% heading and photoperiod sensitivity indices (Kp) from ICRISAT Bamako research station trials.

Entry number	Name	Type†	Grain yield Mg ha ⁻¹	Difference over Tieble	Superiority %	Mean plant height cm	50% heading‡ Julian d	Kp§
9	Pablo	Hyb	1.92	0.28	17	317	265	0.91
13	Caufa	Hyb	1.86	0.21	13	323	266	0.92
11	Omba	Hyb	1.85	0.20	12	343	268	0.88
15a	Wagui¶	Hyb	1.78	0.14	8	345	—	—
12	Niakafa	Hyb	1.75	0.10	6	343	264	0.81
14	Teli	Hyb	1.75	0.10	6	310	263	0.81
10	Yamasa	Hyb	1.70	0.06	3	342	268	0.75
8	Jamajigi	PLEC	1.63	-0.02	-1	193	271	0.75
7	Fatoma	PLEC	1.48	-0.17	-10	329	255	0.30
5	Kemessou	PLEC	1.46	-0.18	-11	284	258	0.58
2	Sotigui	PLEC	1.45	-0.20	-12	324	257	0.33
1	Babalissa	PLEC	1.34	-0.30	-18	269	249	-0.03
6	Keneya	PLEC	1.33	-0.32	-19	311	256	0.54
3	Kolo	PLEC	1.31	-0.33	-20	310	257	0.21
4	Kamalen	PLEC	1.22	-0.42	-26	324	258	0.28
15b	DouaG¶	LVC	1.58	-0.07	-4	—	272	0.91
16	Tieble	LVC	1.65	—	—	332	269	0.80
LSD (5%)				0.11	7	14		

† Hyb, hybrid experimental cultivar; PLEC, pure-line experimental cultivar; LVC, landrace-cultivar check.

‡ Based on data from 2010 trial sown on 26 June (177 Julian d).

§ Calculated using Eq. [1] and heading dates from 2009 (196 Julian d sowing) and 2010 (177 Julian d sowing).

¶ Wagui was tested only in 2009 and replaced in 2010 and 2011 by DouaG.

Table 4. Genetic (σ_g^2) and genotype-environment interaction (σ_{ge}^2) variance components and grain yields, hybrid to local check 'Tieble' yield comparisons, and plant heights within sets of on-farm trials grouped by trial mean productivity level.

	Trial yield level‡			
	Low	Mid-low	Mid-high	High
Number of trials	7	11	11	8
σ_g^2/σ_{ge}^2 for grain yield‡	3.97*/1.16 ^{NS}	3.30*/2.31 ^{**}	5.56*/2.31 ^{NS}	16.40*/9.48*
Mean yield of individual trials (range Mg ha ⁻¹)	0.78–1.10	1.14–1.50	1.54–1.99	2.07–2.60
Mean yield over all trials (Mg ha ⁻¹)	1.00	1.33	1.73	2.31
Mean yield of Tieble (Mg ha ⁻¹)	0.92 ^{SH}	1.47 ^{NSH}	1.73 ^{NSH}	2.51 ^{NSH}
Mean yield of all hybrids (Mg ha ⁻¹)	1.23	1.51	1.97	2.73
Mean yield of best hybrid (Mg ha ⁻¹)	1.41 ^a	1.63 ^b	2.20 ^c	3.23 ^a
Mean yield of hybrid Pablo§ (Mg ha ⁻¹)	1.35	1.61	2.20	2.85
Mean yield of individual trials (range g m ⁻²)	78–110	114–150	154–199	207–260
Mean yield over all trials (g m ⁻²)	100	133	173	231
Mean yield of Tieble (g m ⁻²)	92 ^{SH}	147 ^{NSH}	173 ^{NSH}	251 ^{NSH}
Mean yield of all hybrids (g m ⁻²)	123	151	197	273
Mean yield of best hybrid (g m ⁻²)	141 ^a	163 ^b	220 ^c	323 ^a
Mean yield of hybrid Pablo§ (g m ⁻²)	135	161	220	285
Yield superiority of all hybrids over Tieble (%)	33.7	2.7	13.9	8.8
Yield superiority of hybrid Pablo§ over Tieble (%)	46.7 ^{**}	9.5 ^{NS}	27.2 ^{***}	13.6 ^{**}
Pairwise comparisons of hybrid vs. Tieble (total count)	44	70	71	45
Pairwise comparisons with significant ($P < 0.05$) hybrid yield inferiority relative to Tieble (%)	2.3	4.3	7.0	0.0
Pairwise comparisons with significant ($P < 0.05$) hybrid yield superiority relative to Tieble (%)	31.8	18.6	28.2	17.8
Mean plant height¶ Tieble (cm)	292	299	368	406
Mean plant height¶ all hybrids (cm)	285	306	346	401
Mean plant height¶ of within group highest yielding hybrid (cm)	293 ^a	315 ^b	345 ^c	393 ^a
Mean plant height¶ hybrid Pablo§ (cm)	267	289	345	389

* Significant at the 0.05 probability level.

** Significant at the 0.01 probability level.

*** Significant at the 0.001 probability level.

† NS, not significant ($\alpha = 0.05$); SH, significantly different from hybrid mean yield, at $\alpha = 0.01$; NSH, not significantly different from hybrid mean yield; a, Caufa was best hybrid; b, Omba was best hybrid; c, Pablo was best hybrid.

‡ Variance components were multiplied by 100 for better readability.

§ Hybrid with highest yield across all 37 trials.

¶ Only available for 2009 trials, with two, four, five, and two trials respectively for low-, mid-low-, mid-high-, and high-yielding groups.

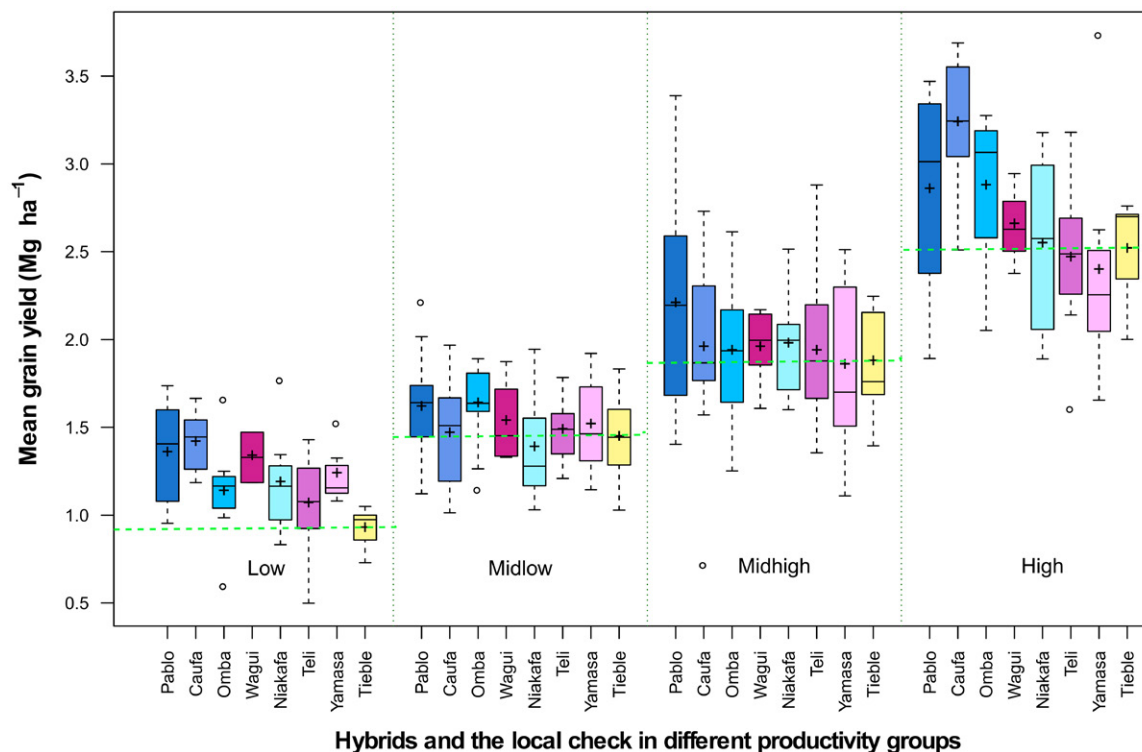


Fig. 2. Individual trial grain yields (Mg ha^{-1}) of hybrids and the local check 'Tieble' within productivity level (see Table 4) presented as boxplots where the midline denotes the genotype median, the colored box corresponds to 25% above and 25% below the median, the plus sign denotes the mean, whiskers indicate the total range, and circles show outlier values. Genotypes are sorted within productivity levels based on their overall mean grain yield. The hybrid Wagui was only tested in 2009 and present in two, four, five, and two trials in the low-, mid-low-, mid-high-, and high-yielding groups, respectively.

similar dynamic stability estimates and showed an additive behavior paralleling the environmental trend lines, and Pablo's superiority over Tieble remained constant. Caufa ($b = 1.49$) and Yamassa ($b = 0.91$), in contrast, showed substantially higher and lower dynamic yield stability than Tieble, respectively, with their yield superiorities over Tieble increasing in the higher- (Caufa) and lower-yielding (Yamassa) environments.

The minimum hybrid yield superiority required for farmers to recover the seed price was calculated to be 0.05 Mg ha^{-1} based on the cost of seed (1.55 € kg^{-1} , the current maximum retail price), a conservatively high estimate of seed required to sow one hectare (5 kg), and the farm-gate price for grain at harvest time (0.15 € kg^{-1}). The hybrid yield superiorities over Tieble were, on average, higher than this break-even value for all of the eight hybrids (across all 37 environments) (Table 3). The overall highest-yielding hybrid, Pablo, had mean yield superiorities higher than the break-even point in all four yield-productivity groups (Table 4), as did Omba and Wagui.

All experimental pure line varieties yielded less than Tieble, with 0.02 to 0.42 Mg ha^{-1} (1–26%) yield inferiorities averaged across the 37 trials. The second local check variety, DouaG, also yielded slightly less than Tieble.

The plant height of all experimental hybrids and pure-line varieties (except Jamajigi) was $>3 \text{ m}$, similar to Tieble (Table 3). The experimental hybrids exhibited photoperiod

sensitivity similar to both local checks, with K_p values varying between 0.75 and 0.92 (Table 3). In contrast, seven of the eight PLECs showed considerably less photoperiod-sensitivity indices (ranging from -0.03 to 0.58), with only Jamajigi being similar to Tieble. All photoperiod-sensitive varieties matured in the same period as Tieble, whereas the less photoperiod-sensitive varieties matured earlier, as indicated by their earlier heading dates (Table 3).

DISCUSSION

Pertinence of Results for Smallholder Sorghum Producers in WCA

The wide range of sowing dates, rainfall, cultural practices, soil types, and productivity levels sampled in this study allowed a robust assessment of the tall guinea-race sorghum hybrids for performance under smallholder sorghum producers' cultivation environments in Mali. The repeatabilities of the single on-farm trials for grain yield were generally high (Supplemental Table S2), indicating the statistical relevance of this dataset and the quality of the data obtained from on-farm trials. They also showed the feasibility of effectively discriminating among contrasting genotypes under low- and high-productivity conditions in these on-farm yield trials, as was previously reported by Rattunde et al. (2013, 2016).

Although fertilizer was provided to farmers to help obtain better repeatabilities under the frequently heterogeneous field conditions, the productivity levels still covered

the spectrum from below the current Malian average of 1.0 Mg ha⁻¹ (FAOSTAT, 2015) to well over double that level. Farmers were free to apply the fertilizer according to their own practice, resulting in many applications after the first weeding, as is typical, and thus often too late for the applied phosphorus (P) to benefit that year's growth (Schenk and Barber, 1979; Nord et al., 2011).

Tieble, the local check used in our study, is widely cultivated by Malian farmers and exhibited stable grain yield across the heterogeneous cropping conditions in this study (Fig. 1). It thus provided a good standard for comparing productivity of the new tall hybrids.

Extent and Nature of Genotype-by-Environment Interaction

The GEI across all environments was significant but poorly explained by factors such as productivity, year, or zone. Overall, the significant GEI variance was smaller than genotypic variance (Table 2) and appeared to be primarily attributable to interaction at the individual farmer-field level, as was previously observed in trials of shorter hybrids (Rattunde et al., 2013); hence, there is no a priori need to examine hybrid performances within specific mega-environments, but the differences in hybrid superiority relative to the local check across productivity levels suggested that testing across an ample range of on-farm productivity conditions would be worthwhile.

Tall Hybrid On-Farm Yield Performance

The yield superiorities of the tall hybrids over the well-adapted local variety Tieble were sufficiently large to be of importance to sorghum farmers in WCA. The 0.28-Mg ha⁻¹ average yield superiority of the best hybrid Pablo (Table 3) was substantial in comparison to farmers' typical yields of only 1.00 Mg ha⁻¹ in Mali (FAOSTAT, 2015). Furthermore, the relative yield superiorities were even larger in the lowest-productivity conditions (Table 4), under which the majority of sorghum farmers in Mali grow sorghum (Leiser et al., 2012; Rattunde et al., 2016). Higher yield superiorities of hybrids over pure-line check varieties under stressed environments were previously observed in sorghum (Hausmann et al., 1998) and other crops (Bidinger et al., 1994; Tollenaar and Wu, 1999; Betrán et al., 2003; Yadav et al., 2014).

The yield superiorities of the tall hybrids were, in general, smaller than those of shorter-stature hybrids (Rattunde et al., 2013), averaging only 9% for tall hybrids across all environments (Table 3), as compared with 28% for shorter hybrids (Rattunde et al., 2013). The same was true on the basis of individual hybrids, where the average yield superiority of tall hybrids ranged from 3 to 17% (0.06–0.28 Mg ha⁻¹), whereas for shorter hybrids, it varied from 17 to 37% (0.27–0.60 Mg ha⁻¹) (Rattunde et al., 2013). Yet the yield superiority of tall hybrids equaled or surpassed that

of the short hybrids under the lowest-productivity conditions (averaging 34% for tall hybrids and 24% for short hybrids). Thus, a major difference between tall and short hybrids appears to be the greater yield response to improved productivity conditions by short hybrids as compared with tall hybrids. The short hybrids, however, maintained a stable yield superiority, expressed on a percentage basis, over increasing productivity levels (Rattunde et al., 2013), whereas the tall hybrids only exhibited a constant absolute yield superiority (Supplemental Fig. S2).

Comparisons between the tall and short sorghum hybrids is facilitated by their having been evaluated across a similar sample of environments, with trials of tall hybrids and short hybrids conducted in the same villages each year. Also, Tieble was used in both trial series, as the check and its average yield were nearly identical across both the short (1.64 Mg ha⁻¹) and tall hybrid (1.65 Mg ha⁻¹) trial series. The mean yield of Tieble did differ between the set of trials classified as low productivity for the short- (1.16 Mg ha⁻¹) and tall-hybrid trials (0.91 Mg ha⁻¹), but it was comparable when the tall hybrid experiments under low and mid-low productivity levels were averaged (1.20 Mg ha⁻¹, Supplemental Table 5). Thus, for a more appropriate comparison of short and tall hybrids under low productivity conditions, the tall hybrid yields were averaged across low and mid-low productivity levels (Supplemental Table S4 and S5). Using this new low-productivity grouping of tall hybrid environments, the best tall hybrid, Pablo, showed 24% yield superiority over Tieble, whereas the best short hybrid, Fadda, exhibited 32% superiority over Tieble under low-productivity conditions, despite both hybrids having the same male parent.

The different yield response of tall versus short hybrids is expected to have a physiological basis, as there were no observable differences for frequency of lodging. van Oosterom and Hammer (2008) observed that a short sorghum hybrid exhibited larger increases in grain number in favorable environments, as measured by growth rates at anthesis under increasing nitrogen availability compared with a tall hybrid. This difference was attributed to differential partitioning of dry matter to the reproductive tissue.

Despite the relatively larger yield advantage of short sorghum hybrids, factors such as competitiveness with weeds (Traore et al., 2003) and the preference for and possible benefit of taller plant types for reducing risks of transhumant cattle grazing and bird damage may still lead farmers to grow tall hybrids. Furthermore, because sorghum is mostly produced under low soil-P conditions in WCA, the actual height attained may be considerably less than its genetically potential height, with low P reducing sorghum height by 1 m or more (Leiser et al., 2015). For example, the height of tall hybrids in the lowest-productivity group of this study averaged only 285 cm as compared with 401 cm in the highest-productivity group (Table 4). Thus, these tall

hybrids, even under low-productivity conditions, are able to exceed the minimum height (2.5 m) needed to avoid losses from animal grazing at maturity. Examination of the relative economic values of taller, likely higher-biomass plant types versus shorter sorghum plant types with potentially higher stover digestibility for livestock feed would be worthwhile, particularly based on initial results that show a 1.1% ($P < 0.001$) increase of *in vitro* digestibility for each centimeter reduction of stem internode length (F. Rattunde, personal communication, 2016).

Risks and Opportunities of Producing Tall Sorghum Hybrids

The new tall hybrids should represent a low risk of yield inferiority relative to local, well-adapted varieties for farmers needing to choose between these two options. Furthermore, the frequency of inferiority was even lower (2.3%) (Table 4) in the lowest-productivity trials that corresponded to the most common sorghum production conditions in WCA. The highest-yielding hybrid had only a single case of significant yield inferiority in 37 trials, and this occurred under higher, less typical production conditions.

The minimum hybrid yield superiority required for farmers to recover the seed price was actually very low, being only 0.05 Mg ha⁻¹. Thus, farmers' risk of not recouping the value of their investment in purchased seed of a new tall sorghum hybrid is small. Furthermore, the results of this study are conservative, as the experimental hybrids tested here resulted from very weak selection intensity and a small number of parental lines with no prior combining ability testing. A dedicated full-scale hybrid breeding program with larger numbers of parental lines, higher selection intensities, and broader genetic diversity can be anticipated to produce even larger hybrid yield superiorities and lower risks of hybrid yield inferiority for smallholder farmers.

Already, both male and female farmers in Mali have access to seed of the guinea-race hybrids tested in this study (Weltzien et al., 2010), and adoption is increasing (Smale et al., 2014) despite farmers' unfamiliarity with hybrid seed and the cultural norm of not purchasing sorghum seed. The annual doubling of hybrid sorghum seed production by farmer seed-producer organizations during the past 6 yr in Mali attests to the interest in and adoption of guinea-race hybrid sorghum (E. Weltzien, personal communication, 2016).

A driver for the interest and adoption of the new guinea-race sorghum hybrids is the yield superiorities that have not been matched by formally bred pure-line varieties. The 0.43-Mg ha⁻¹ yield superiority of Pablo under the lowest productivity level of approximately 1 Mg ha⁻¹ (Table 4) can make the difference between food insecurity and food security plus income for smallholder farmers. Hybrids, which in addition to higher yields have farmer-preferred characteristics

such as taller height, lax panicles, and good grain quality and storability, represent a truly new option for WCA farmers that should be pursued by properly scaled hybrid breeding programs. The balance between sufficient plant height and the greater yield potential of shorter hybrids could be examined with medium tall hybrids, particularly when breeding for farmers operating under low-input conditions.

CONCLUSIONS

From the advances in Malian sorghum hybrid development and adoption of these farmer-preferred hybrids, it can be concluded that guinea-race sorghum hybrid breeding is a very promising strategy to help improve the livelihood of many smallholder farmers. Hybrids that have, in addition to higher yields, farmer-preferred characteristics, such as taller height, lax panicles, and high seed or grain quality, should be pursued in breeding programs. These hybrids bear a great potential to boost grain yield production under smallholder farmers' low-productivity conditions, because these hybrids will be adopted by farmers and thus will not be a mere scientific advancement. For future efforts, medium tall hybrids that have all the other farmer-preferred traits and are specifically bred for low-input conditions can be considered. Such hybrids would have most probably a higher harvest index and would still show a high adoption rate among farmers.

Conflict of Interest

The authors declare there to be no conflict of interest.

Supplemental Material Available

Supplemental material for this article is available online.

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