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Evaluation of Relative Competitive Ability and Fitness of *Sorghum bicolor*×*Sorghum halepense* and *Sorghum bicolor*×*Sorghum sudanense* F_1 Hybrids

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ABSTRACT
Introgression of crop alleles in weedy sorghum populations may have an additive effect on the adaptive character of the weeds making them more competitive. The relative fitness in the F_1 generation derived from weedy and crop sorghums was evaluated using competitive assays in densely planted plots. Replacement series assays were utilized to evaluate the competitiveness of the F_1 in the greenhouse and in the field. Interspecific crosses between *S. halepense*×*S. bicolor* and *S. sudanense*×*S. bicolor* showed vigour in vegetative morphological parameters. Tillering, plant height at maturity and plant weight of the F_1 increased up to 70, 50 and 100%, respectively. The analysis of reproductive fitness associated traits showed that the hybrids had Relative Crowding Coefficients (RCC) values of between 5.2 and 10.1 on the number of panicles per plant. High RCC values of up to 76.9 on the number of seeds per plant and values of up to 19.5 on the total seed weight were observed in the hybrid indicating that the hybrid was more competitive than the parents. The *S. halepense*×*S. bicolor* F_1 progenies had less seed produced when grown in competition with *S. bicolor* and an RCC of 4.3 was observed. Ratooning was reduced in the F_1 of *S. halepense*×*S. bicolor* when grown in competition with *S. halepense* and an RCC of 5.0 was observed. The F_1 hybrid of *S. sudanense*×*S. bicolor* had significantly more panicles (6.3) than *S. bicolor* (1.9) but it was not different from *S. sudanense* (6.0). Both F_1 populations had high levels of seed dormancy and forced germination gave 53% in *S. halepense*×*S. bicolor* and 69% in *S. sudanense*×*S. bicolor* which gave low values as compared to their parents. Results from the study indicate that the release of improved transgenic varieties should be preceded by investigation on the effect of their interaction with weedy members in the sorghum genus.

Key words: Relative crowding coefficients, *Sorghum bicolor*, *Sorghum halepense*, *Sorghum sudanense*, relative fitness

INTRODUCTION

Crop genes introgressed into their wild relatives may possibly confer an adaptive advantage or penalty to the crop weed hybrid as a consequence of acquired plant features that may of enhance or diminish its fitness. This advantage or penalty to the hybrid can influence the vegetative and/or the reproductive phase of the plant (Dale, 1994). Crop genes in weedy species may enhance plant fitness traits such as, levels of seed dormancy, mode of reproduction, nature of specific habitat and nature of competition. The persistence of hybrid weeds depends on their relative fitness and the levels of competition they may endure (Dale, 1994). Persistence of crop alleles in the weedy background may render the hybrid more invasive and increase the chance of hybridization and flow of robust crop alleles to both the hybrid and weedy populations. Interactions between crop genes and wild genes in sorghum weeds may also increase the selective advantage, invasiveness or weediness in the wild sorghum populations (Hokanson *et al*., 2010).

Studies on the potential invasiveness of crop wild hybrids in traditional agricultural systems show that fitness of crop×weed hybrids vary across crop species (Ellstrand, 2003) and across different agro-ecological environments (Chapman and Burke, 2006). Studies on hybrids of crop and wild rice showed increased heterosis for the vegetative production when compared to the parents (Langevin *et al*., 1990). Wild radish and crop radish hybrids showed greater seed set than non hybrids (Ellstrand, 2003). However, Arriola and Ellstrand (1997) found insignificant differences in the reproductive and vegetative competitiveness of *S. halepense*×*S. bicolor* hybrids as compared to *S. halepense* and *S. bicolor* monocultures.

Hybrids derived from different species in the same genus have been reported to have greater adaptive advantage due to enhancement of important vegetative features. Song *et al*. (2004) obtained an F_1 population from crossing *O. sativa* and *O. rufipogon* and showed that the F_1 had slightly higher hybrid vigour at the vegetative growth phase and better tillering than the parents. Crop by wild hybrids in lettuce have shown higher vigour than their parents and the resulting heterosis has potential of increasing fitness of their offsprings (Hooftman *et al*., 2009). This has also been shown in the F_1 in response to drought, salt and nutrient deficiency environments (Uwimana *et al*., 2012).

Studies within Poaceae have shown that F_1 hybrids between round-up-ready corn with teosinte showed significantly higher vegetative vigour than that of teosinte (Guadagnuolo *et al*., 2006). The F_1 hybrids obtained did not exhibit a direct or negative impact of the transgene on reproductive fitness in the absence of selective pressure from glyphosate (Guadagnuolo *et al*., 2006). F_1 hybrids between crop sorghum and shattercane exhibited higher vegetative vigour and higher biomass production as compared to the parents (Sahoo *et al*., 2010). However, the hybrid between shattercane×*S. bicolor* did not show any difference in ecological reproductive fitness with its parents (Sahoo *et al*., 2010). In addition, Mercer *et al*. (2006) showed that sunflower F_1 hybrids were less fecund than wild plants, yet more likely to survive to reproduce. In addition crop×wild hybrids in sunflower showed greater relative fitness when grown under competitive conditions (Mercer *et al*., 2006). Fitness in crop×wild lettuce F_1 hybrids and backcross populations also seemed to show similar or higher vigour compared to the parents (Uwimana *et al*., 2012). Transgressive segregation leading to hybrid vigour in the F_1 derived from genetically distant but conspecific crop species is a vital aspect to consider while determining the role of transgenes in non target plant populations.

The vigour in the F_1 due to interspecific hybridization may boost plant features associated with enhancing fecundity in the hybrid population. The change in fecundity has been observed in some studies. Wild radish×crop radish F_1 population showed 27% greater fecundity and 22% greater survival than wild plants in some environments (Campbell *et al*., 2006). However, evaluation of the F_3 population showed fewer seeds per fruit produced and fewer fruits per flower set than in the wild plants, resulting in lower lifetime fecundity (Campbell and Snow, 2007). A study of wild by crop hybrids of squash showed relative fecundities of between 15-53% as compared to the wild plants (Spencer and Snow, 2001). The effect of interspecific hybridization on vegetative fitness and fecundity suggests that the crop alleles can persist within introgressing populations over several generations. The F_1 population therefore does not represent a barrier to introgression of neutral, null or beneficial alleles (transgenes) into weedy or wild sorghum populations.

It is imperative to define ways of evaluating the effect of transgenes on fitness of crop, wild relatives and their hybrids. The most important parameters to consider include; plant vigour, biomass production, seed production, seed dormancy and resistance or tolerance to given biotic pressures. The study determined and compared the relative competitive ability, fitness and fecundity of the *S. halepense*×*S. bicolor* and *S. sudanense*×*S. bicolor* hybrids.

MATERIALS AND METHODS

Competitive study of F_1 hybrids and parents in the greenhouse: Vegetative and reproductive fitness of *S. bicolor*, *S. halepense*, *S. sudanense* and their hybrids obtained from weed to crop crosses was tested using a competitive approach. Dense planting (4 plants in a 30 cm pot) with altered crop, weed and hybrid mixture ratios in greenhouse pots were applied to evaluate significant advantage among the weed-crop hybrids. The experiment was sited at the College of Agriculture and Veterinary Sciences (CAVS) (-1°14’59.72", +36°44’30.79"). Seeds from *S. bicolor*, *S. halepense*, *S. sudanense* and their hybrids were germinated by subjecting them to temperatures of 5°C for 10 days then to 45°C for 24 h in a drying oven to break dormancy (Holm *et al*., 1977). Two weeks after germination, the seedlings were transplanted into 30 cm diameter pots filled with growth medium mixture (3 parts loamy soil; 1 part sand and 1 part manure).

Plants were watered twice a day trough drip irrigation and maintained at 12/12 h day/night photoperiod and at 28/24°C day/night temperatures throughout the growth period. The plants were fertilized three times per week through fertigation. A starter fertilizer mixture Polyfeed® NPK, 19:19:19 from Amiran Kenya (95 $\mu g\ L^{-1}$ nitrogen, phosphorus and potassium per day) was applied for 30 min two times a day and three times a week in irrigation water from germination till the onset of flowering. This was followed by a finisher fertilizer mixture Polyfeed® NPK, 18:9:27 from Amiran Kenya (90 $\mu g\ L^{-1}$ nitrogen, 45 $\mu g\ L^{-1}$ phosphorus and 67.5 $\mu g\ L^{-1}$ potassium per day) that was applied for 30 min, two times a day and three times a week in irrigation water until flowering stage. Plants were watered twice a day trough drip irrigation and maintained at 12/12 h day/night photoperiod and at 28/24°C day/night temperatures throughout the growth period. Insect pests, such as cutworms, spider mites and stem borers were controlled. A miticide Ortus®, SC 5% (fenpyroximate) was applied as a foliar spray at a rate of 0.05 kg ha^{-1} during mite infestation. A pesticide Dursban® 50 W (chlorpyrifos) was used to control lepidopteran and homopteran pests at a rate of 0.28 kg ha^{-1}. Polytrin® P440 EC was applied at 1.0 L ha^{-1} to control lepidopteran and homopteran and mites. Greenhouse conditions varied between 28-20°C day/night temperature and 12/12 h day/night photoperiod. Dense planting with 4 plants in a 30 cm pot was used in the replacement series to obtain competition through out the life cycle, but allow the plants to flower and to fruit.

In the replacement series design (Radosevich, 1987), different plant density ratios were utilized to assay the competitiveness of one genotype against the other and thus study the advantage or penalty of hybrids between weeds and crop. Plants were raised in pots in the greenhouse, in an RCBD design with 4 replications. Percent parent to hybrid ratios of 100:0, 75:25, 50:50, 25:75 and 0:100 were randomized in each of the 4 blocks. Plant competitions were categorized as follows: *S. bicolor* grown in competition with *S. bicolor*×*S. sudanense* hybrids, *S. sudanense* grown in competition with *S. bicolor*×*S. sudanense* hybrids, *S. bicolor* grown in competition with *S. bicolor*×*S. halepense* hybrids and *S. halepense* grown in competition with *S. bicolor*×*S. halepense* hybrids. Plants were established at the following crop or weedy relative: hybrid mixture ratios: 4:0, 3:1, 2:2, 1:3 and 0:4 per pot, where 4 plants per pot represented 100%, 3 plants; 75%, 2 plants; 50% and 1 plant 25%. In total 20 *S. halepense* plants (8 in monoculture 12 in mixed cultures), 20 *S. sudanense* plants (8 in monoculture 12 in mixed cultures) and 40 *S. bicolor* plants (16 in monoculture 24 in mixed cultures) were grown and assayed. The linear model applied for the analysis of variance considered the treatment effect, block effect, treatment×block effect and a random element of variation as in Eq. 1 below:

$$Y_{ij} = \mu+\tau_i+\beta_j+\gamma_{ij}+\varepsilon_{ij} \quad (1)$$

where, μ value common to all data points, τ_i is the treatment effect, β_j is the block effect, γ_{ij} is the treatment effect×block interaction effect and εij is a random element of variation.

Data collection and analysis: The Relative Crowding Coefficient (RCC) was used to measure the competitive ability and as a measure of the competitive ability of one genotype to obtain limiting resources of solar, nutrition and water when grown in mixtures with another genotype. This is compared with the ability of the genotypes to use those resources when grown in a pure stand (Hunt, 1978; Novak *et al*., 1993; Massinga *et al*., 2005). The RCC for biomass production for *S. bicolor* and *S. bicolor*×*S. sudanense* hybrid was calculated as shown in Eq. 2 below:

$$\text{RCC} = \frac{B(4:0\text{ hybrid})}{B(4:0\text{parent})}+\frac{B(3:1\text{ hybrid})}{B(3:1\text{parent})}+\frac{B(2:2\text{ hybrid})}{B(2:2\text{parent})}+\frac{B(1:3\text{ hybrid})}{B(1:3\text{parent})} \quad (2)$$

where, B (4:0 hybrid) and B (4:0 parent) represented biomass production in plots with 100% hybrid and parent, respectively. The B (3:1 hybrid) and B (3:1 parent) represented biomass production in plots with 75% hybrid and parent respectively. The B (2:2 hybrid) and B (2:2 parent) represented biomass the production in plots with 50% hybrid and parent, respectively. The B (1:3 hybrid) and B (1:3 parent) represented biomass production in plots with 100% hybrid and parent, respectively. Total biomass production including, plant height, number of tillers, time to flowering, grain yield were measured and Photosynthetic Active Radiation (PAR). A quantum light probe was used to measure the photon flux in the PAR at a wavelength range from 400-700 nm. Adaxial and abaxial readings were taken and the difference was determined as the actual PAR. The readings were taken over a 150 day period in 10 day intervals. The PAR was defined in terms of photon (quantum) flux, calculated as the number of moles of photons in the radiant energy. A germination test was carried out on the seeds from the hybrids to determine their viability. Plant height and number of tillers were analyzed using regression analysis. The regression slope and *y* intercepts were compared using t tests. Leaf and stem dry weight, grain yield and rhizome production parameters were analyzed using analysis of variance and mean differences between the genotypes were compared at $p \leq 0.05$ in GENSTAT 14.

RESULTS

Morphological differences at maturity (150 days) of *S. sudanense*, *S. halepense*, *S. bicolor* and their hybrids grown in competition: Experimental plants grown in competition in the replacement series designs showed significant differences among parents and their F_1 progenies ($p \leq 0.05$) (Table 1). Total plant weight in both F_1 populations of *S. halepense*×*S. bicolor* (426 g) and of *S. sudanense*×*S. bicolor* (424.1g) was higher than that of their three parents *S. halepense* (213.8 g), *S. bicolor* (241.7g) and *S. sudanense* (293.7g) (Table 1). Photosynthetic active radiation was highest in *S. sudanense* (110.17) while *S. bicolor* and the F_1 between *S. halepense* and *S. bicolor* had PAR of 92.15 and 99.6, respectively while *S. sudanense*×*S. bicolor* had a PAR of 88.64. The least PAR was recorded in *S. halepense* (88.28) (Table 1). There were more tillers in the *S. sudanense*×*S. bicolor* F_1 (3.362) and one of their parents, *S. sudanense* (3.345). *Sorghum sudanense*×*S. bicolor* had average number of tillers (2.257) while both *S. bicolor* and *S. halepense* had the least number of tillers with means of 1.083 and 1.505, respectively (Table 1). Branches above the second internode were more frequent in *S. sudanense* (mean of 0.3) and it's F_1 with *S. bicolor* (mean of 0.2). *Sorghum halepense*, *S. bicolor* and their F_1 had mean branching of less than 0.08. Differences in the total height of the experimental genotypes were significant ($p \leq 0.05$) (Table 1). The mean height of *S. bicolor*, *S. halepense* and their F_1 were recorded at 111.8, 78.5 and 120.6 cm, respectively. *Sorghum sudanense* showed total height of 135.8 cm at maturity while the F_1 progenies between *S. sudanense* and *S. bicolor* had a mean height of 144cm at maturity (Table 1).

The mean number of leaves at maturity ranged between 5-6 in all the parents and F_1 progenies. Above 1 cm culm widths were recorded in *S. bicolor* while the F_1 progenies between weedy species and *S. bicolor* showed widths of between 0.98 and 0.99. Thinner culms were seen in the weedy species *S. halepense* (0.92 cm) and *S. sudanense* (0.975 cm). The number of days the genotypes took to half bloom showed variation, with *S. halepense* giving a mean of 90-95 days and its F_1 with *S. bicolor* attaining half bloom in 70-80 days from germination. *Sorghum bicolor*, *S. sudanense* and the F_1 attained half bloom in between 80-90 days. The percentage flowering also had similar distribution in the genotypes with *S. halepense* showing 65.1% flowering on all main stems, tillers and branches. The results showed that 86.9% stems in *S. halepense*×*S. bicolor* flowered at maturity while 99.1% of all *S. bicolor* had flowered at maturity. *Sorghum sudanense* and its F_1 with *S. bicolor* had flowering on 95.5 and 96.9% of stems (Table 1).

Table 1: Vegetative phase morphological (at maturity-150 days) differences between study species grown in competition

Phenotype	Sb	Sh	Ss	Sh×Sb	Ss×Sb	S.e.d
Number of plants	252	105	120	243	240	
Total plant weight (g)	241.7	213.8	293.7	426	424.1	33.81
Par	92.15	88.28	110.17	99.6	88.64	2.478
Tillers	1.083	1.505	3.345	2.257	3.362	0.1497
Branches	0.017	0.087	0.3	0.088	0.197	0.0577
Height (cm)	111.8	78.5	135.8	120.6	144	4.43
Number of leaves	5.983	5.524	5.955	5.694	5.933	0.0476
Flowering (%)	99.1	65.1	95.5	86.9	96.9	3.57
Days to half bloom	80-90	90-95	80-90	70-80	80-85	
Culm width (cm)	1.041	0.9214	0.9755	0.9885	0.9917	0.01196

Sh: *Sorghum halepense*, Ss: *Sorghum sudanense*, Sb: *Sorghum bicolor*

Morphological differences during growth phase (150 days) between *S. halepense*, *S. bicolor* and *S. halepense*×*S. bicolor* hybrids grown in competition: Vegetative phase morphological parameters showed significant differences among the experimental species. Branching above the second internode did not begin until day 100 in *S. bicolor*, *S. halepense* and their F_1 (Fig. 1a). Maximum branching was seen at day 110 in *S. halepense* with a mean of 0.3166. However, in *S. halepense*×*S. bicolor* a mean of 0.1799 was obtained while *S. bicolor* had a mean of 0.1. At day 140 mean branching ranged between 0.2-0.5 in the two parents and the F_1 (Fig. 1a). Fast growth in height was seen between day 10 and 80, after which a growth plateau was attained (Fig. 1b). At day 80 *S. bicolor* had a height of 87.75 cm, *S. halepense* had 121.50 cm while *S. halepense* by *S. bicolor* had 143.37 cm. At maturity (day 150) *S. halepense*×*S. bicolor* had a mean height of 164.5 cm, *S. halepense* had 154.5 cm while *S. bicolor* had a height of 108.25 cm (Fig. 1b). *Sorghum halepense* consistently recorded higher culm width from day 20-150 followed by the F_1 between *S. halepense* and *S. bicolor*. *S. halepense* demonstrated thinner stems from day 20-150. However, culm width increase had a plateau at day 80 in all the genotypes (Fig. 1c). The number of leaves increased exponentially from day 20-70 where *S. bicolor* averaged 7.55, *S. halepense* averaged 8.05 while the F_1 progenies of *S. halepense*×*S. bicolor* averaged 8.20. There after senescence associated decline was recorded in all genotypes. At day 150 all genotypes had means of between 5.0-5.25 leaves on the main stem (Fig. 1d). *Sorghum halepense* began flowering on the main stems at between day 60 and 70, as was the case in *S. bicolor*. The F_1 between *S. halepense*×*S. bicolor* began flowering at between day 50 and 60. By day 120, more than 95% of the main stems and the early tillers had flowered (Fig. 1e). Tillers were first seen in *S. halepense*×*S. bicolor* at between day 50 and 60 which peaked at day 110. *S. halepense* had moderate to high tillers through its growth phase, beginning at day 70-150. *Sorghum bicolor* had low tillering that began after day 100 (Fig. 1f).

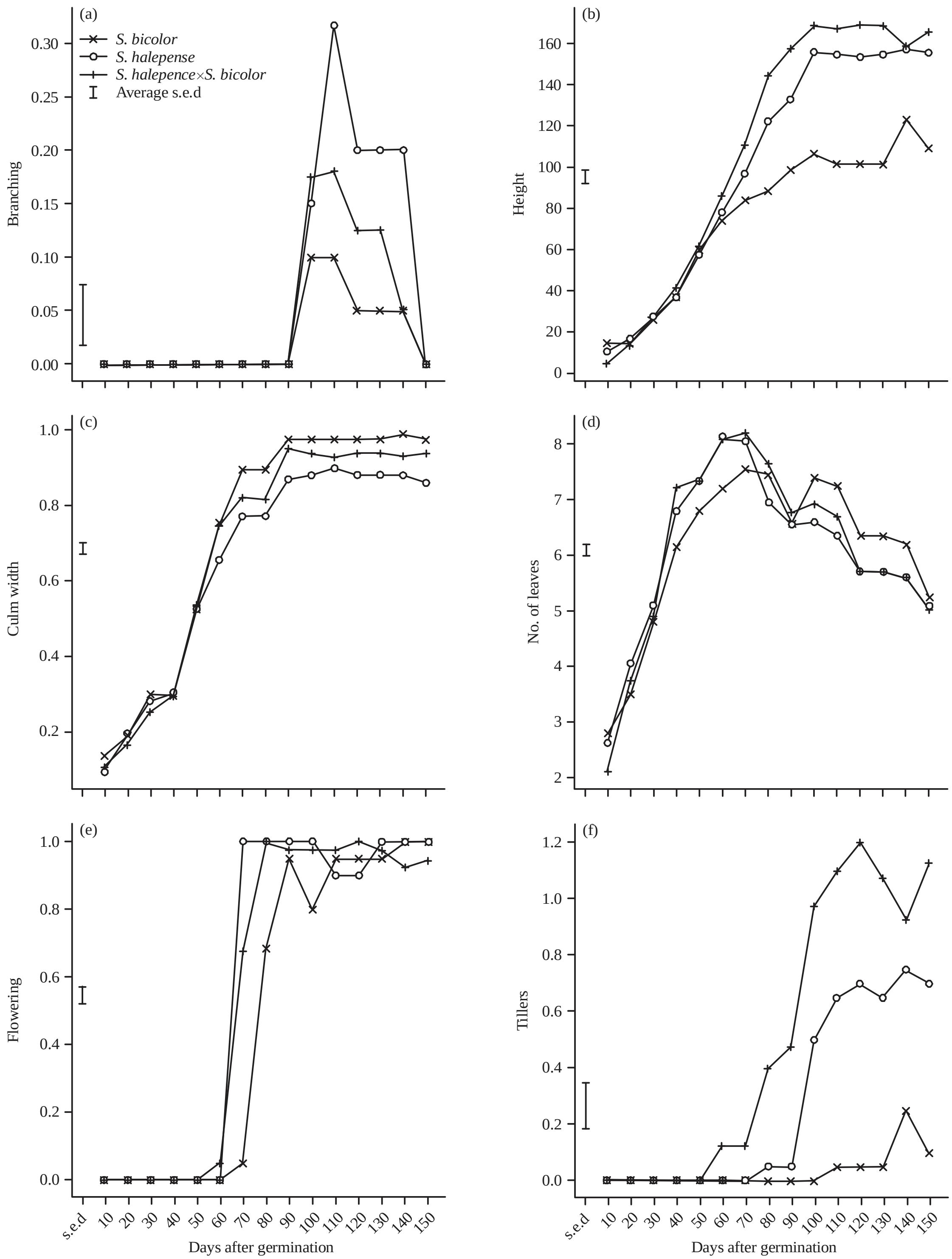

Fig. 1(a-f): Vegetative phase morphological differences among *Sorghum halepense*, *Sorghum bicolor* and their hybrids grown in competition

Morphological differences during growth phase (150 days) between *S. sudanense*, *S. bicolor* and *S. sudanense*×*S. bicolor* hybrids grown in competition: Vegetative parameters exhibited significant differences on the study species grown in competition ($p \leq 0.05$). The F_1 between *S. sudanense*×*S. bicolor* showed significant branching between day 90-150. This was contrary to the situation in the parents where branching was minimal (Fig. 2a). Both parents and F_1

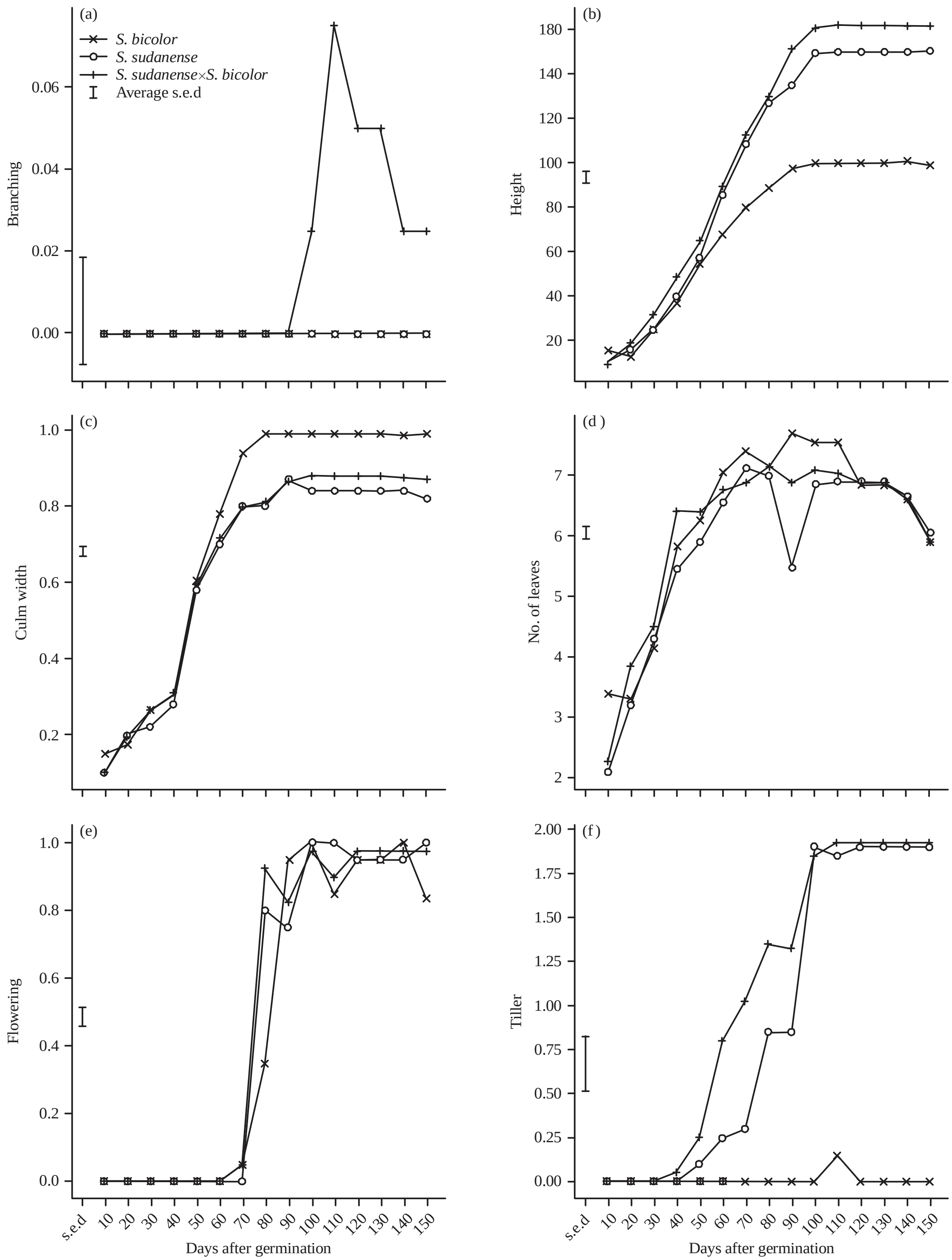

Fig. 2(a-f): Vegetative phase morphological differences among *Sorghum sudanense*, *Sorghum bicolor* and their hybrids grown in competition

progenies achieved their maximum height between days 100 and 110 which was preceded by a fast growth phase between days 20-100 in all cases. *Sorghum sudanense*×*S. bicolor* F_1 progenies consistently showed higher height values than *S. sudanense* and *S. bicolor* (Fig. 2b). Similar fast growth and plateau phases were seen on culm width. Higher width values were seen in *S. bicolor* parent (1 cm) followed by the F_1 progenies of *S. sudanense*×*S. bicolor* (0.9 cm) and the

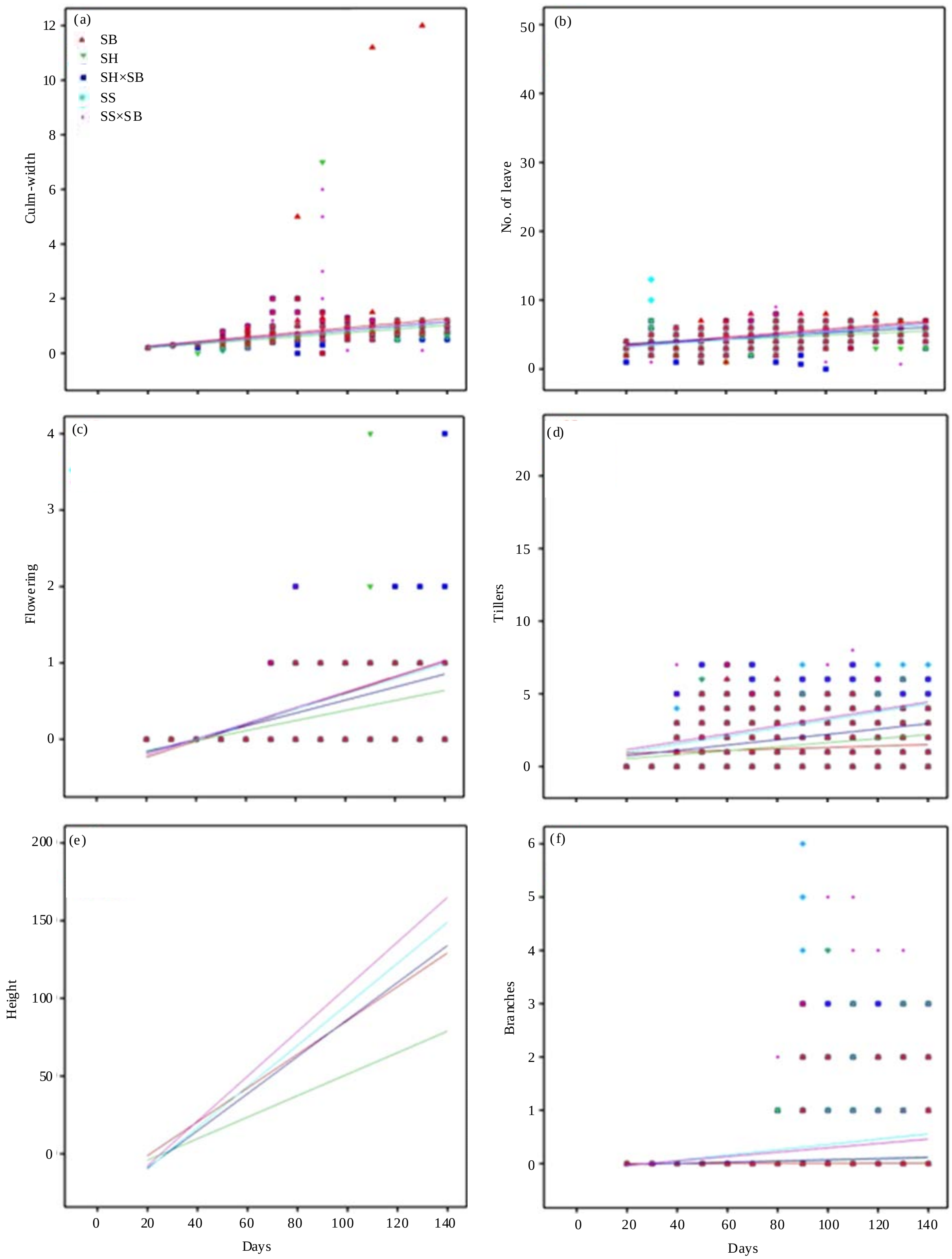

Fig. 3(a-f): Regression analysis for morphological differences among *Sorghum halepense* (SH), *Sorghum sudanense* (SS), *Sorghum bicolor* (SB) and their hybrids grown in competition

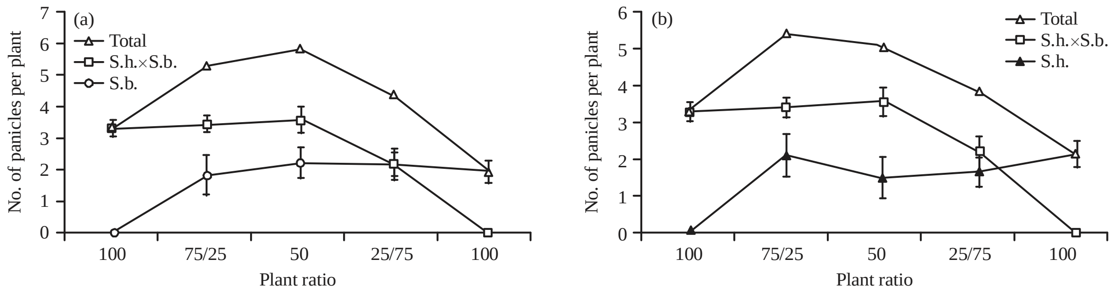

Fig. 4(a-b): Fitness differences on the number of panicles per plant among *Sorghum halepense*, *Sorghum bicolor* and their hybrids grown in competition. Bars represent the standard errors

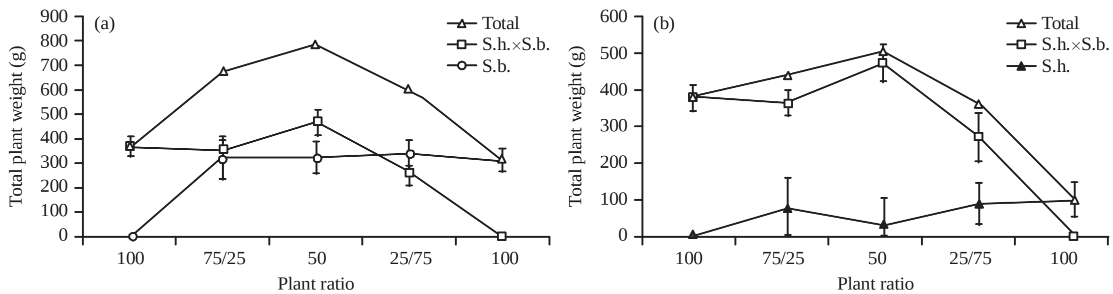

Fig. 5(a-b): Differences on the total plant weight at maturity among *Sorghum halepense*, *Sorghum bicolor* and their hybrids grown in competition. Bars represent the standard errors

S. sudanense parent (0.8 cm) (Fig. 2c). Increase in the number of leaves was fast between days 10 to 60-70. Maximum number of leaves was recorded in *S. bicolor* on day 90 (7.7) *S. sudanense* on day 70 (7.1) and the *S. sudanense*×*S. bicolor* F_1 on day 80 (7.1). By day 150 all genotypes had between 5.9-6.0 leaves as a result of senescence (Fig. 2d).

Flowering in the parents and the F_1 progenies of *S. sudanense* and *S. bicolor* was most expressed between days 60-80. Flowering then had a plateau at day 150 where 100% of *S. sudanense* main stems and tillers had flowered, 97% of *S. sudanense*×*S. bicolor* had flowered and 82% of *S. bicolor* had flowered (Fig. 2e). Tillering began early in *S. sudanense*×*S. bicolor* day 40 and in *S. sudanense* (day 50). Tillering in both genotypes had plateaus at day 100. Low tillering was demonstrated in *S. bicolor* (Fig. 2f).

Regression analysis for morphological differences among *S. halepense*, *S. sudanense*, *S. bicolor* and their hybrids grown in competition: Growth phase parameters and the period of growth (days from germination) showed significant and positive regressions (Fig. 3). Culm width regressed with days from germination in *S. bicolor* had a p-value of <0.001, in *S. halepense* the p-value was equal to 0.069 while in *S. halepense*×*S. bicolor* the p-value was equal to 0.113. Culm width and days from germination in *S. sudanense* and the F_1 from *S. sudanense*×*S. bicolor* had regressions that were not significant. The correlation values for culm width and days from germination were positive and above 0.5 in all genotypes (Fig. 3). Positive regressions and correlations coefficients involving number of leaves, percent flowering and plant height were obtained. The regression relationship involving tillers and branches did not show significant increase with days from planting in all genotypes.

Fitness of *S. halepense*×*S. bicolor* hybrids grown in the field conditions in competition with their parents: Differences on reproductive and fitness related traits among the parents *S. halepense*, *S. bicolor* and the F_1 S. halepense×*S. bicolor* grown in competition were significant ($p\leq0.05$) (Fig. 4a). The mean number of panicles per plant in monocultures of *S. halepense* were 2.17, in *S. bicolor* the number was 1.954 while the F_1 of *S. halepense*×*S. bicolor* had a mean of 3.325 panicles per plant. In crop by hybrid plant mixtures of 25:75 the hybrid had more panicles (3.454). Intersection point was observed at crop by hybrid mixtures of 75:25. This showed increased competitiveness of the *S. halepense*×*S. bicolor* F_1 on the number of panicles as compared to *S. bicolor* (Fig. 4a). A similar situation was seen when *S. halepense* was grown in competition plots with *S. halepense*×*S. bicolor*. The F_1 was more competitive giving an intersection beyond the 25:75-hybrid:weed plant mixture (Fig. 4b). The competitive ability of the *S. halepense*×*S. bicolor* F_1 on total plant weight was more pronounced in competition with *S. halepense* (intersection just before 0:100-hybrid: Crop mixtures) (Fig. 5b) than in competition with *S. bicolor* (intersection just before

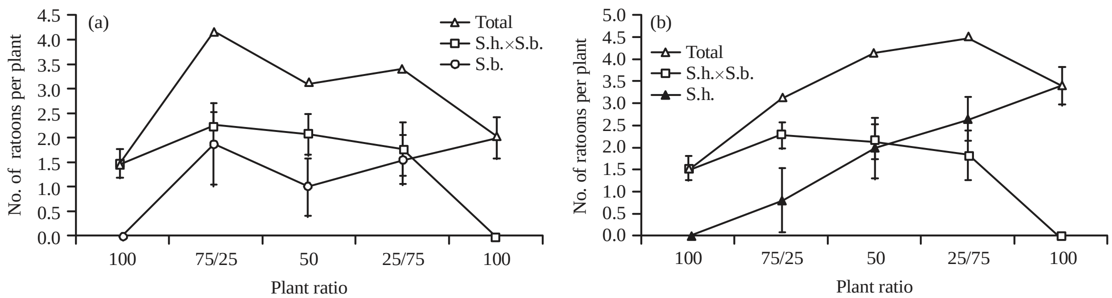

Fig. 6(a-b): Fitness differences on the total number of ratoons per plant among *Sorghum halepense*, *Sorghum bicolor* and their hybrids grown in competition. Bars represent the standard errors

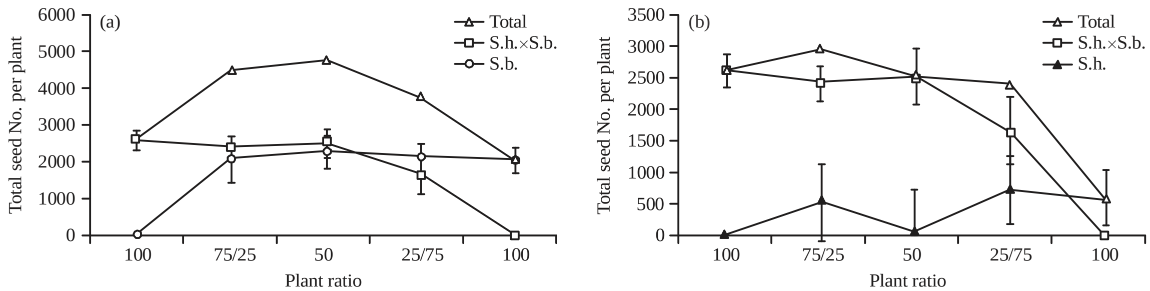

Fig. 7(a-b): Fitness differences on the total number of seeds per plant among *Sorghum halepense*, *Sorghum bicolor* and their hybrids grown in competition. Bars represent the standard errors

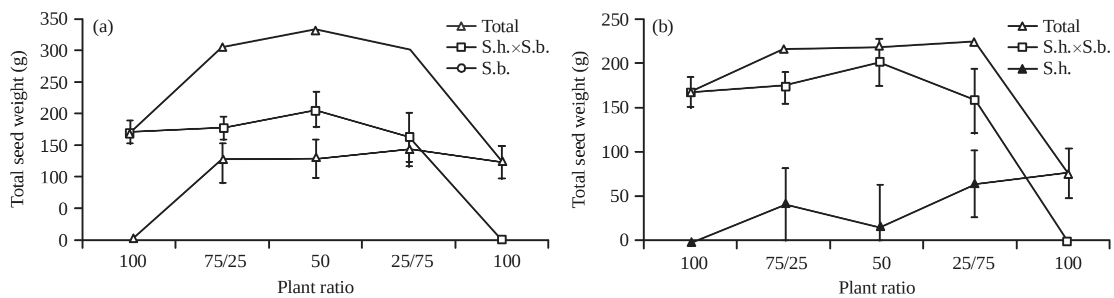

Fig. 8(a-b): Differences on the total seed weight among *Sorghum halepense*, *Sorghum bicolor* and their hybrids grown in competition. Bars represent the standard errors

25:75-hybrid: Crop) (Fig. 5a). Analysis of the number of ratoons showed that the F_1 of *S. halepense*×*S. bicolor* was more competitive than *S. bicolor* parent (intersection after 25:75-F_1: *S. bicolor*) (Fig. 6a). The competitive ability of the F_1 was less pronounced where the *S. halepense*×*S. bicolor* F_1 was grown together with *S. halepense* in competition plots. In this case, the intersection was observed at around 50:50 plant mixture (Fig. 6b). The *S. halepense*×*S. bicolor* F_1 was more competitive than *S. bicolor* on the total number of seed produced per plant. The intersection was seen beyond the 50:50 point (Fig. 7a). Enhanced fitness on seed number was observed in the *S. halepense*×*S. bicolor* F_1. The intersection was towards the 0:100-hybrid:weed crop mixture (Fig. 7b). Enhanced fitness on the F_1 progenies was observed on the total seed weight where the intersection was observed beyond 25:75 in F_1:crop (Fig. 8a) and in F_1:weed plant mixtures (Fig. 8b).

Fitness of *S. bicolor*×*S. sudanense* hybrids grown in the field conditions in competition with their parents: Parental genotypes of *S. sudanense*, *S. bicolor* and the *S. sudanense*×*S. bicolor* F_1 showed significant differences when assayed for reproductive and fitness traits ($p \leq 0.05$) (Fig. 5). Monocultures of the *S. sudanense*×*S. bicolor* (Fig. 9a) had higher number of panicles (5.9) than that of the parental genotypes *S. bicolor* (3) and *S. sudanense* (5). Similarly, *S. sudanense*×*S. bicolor* showed higher fitness under 75:25, 50:50 and 25:75 plant mixtures. The intersection points for both F_1 by crop parent (Fig. 9a) and F_1 by weedy parent (Fig. 9b) were skewed towards 0:100 plant mixtures ratios. The F_1 showed significant fitness than both *S. bicolor* and *S. sudanense* with regard to total plant weight. The intersection was towards 0:100 (F_1: *S. bicolor*) (Fig. 10a) and 0:100-F_1: *S. sudanense* (Fig. 10b) for plant weight.

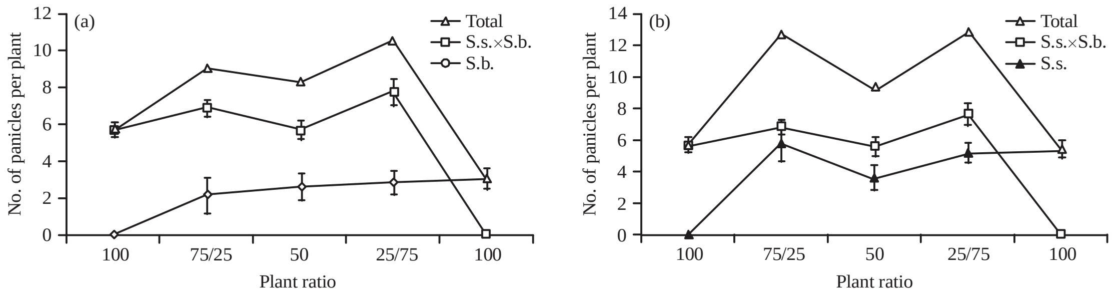

Fig. 9(a-b): Fitness differences on the number of panicles per plant among *Sorghum sudanense*, *Sorghum bicolor* and their hybrids grown in competition. Bars represent the standard errors

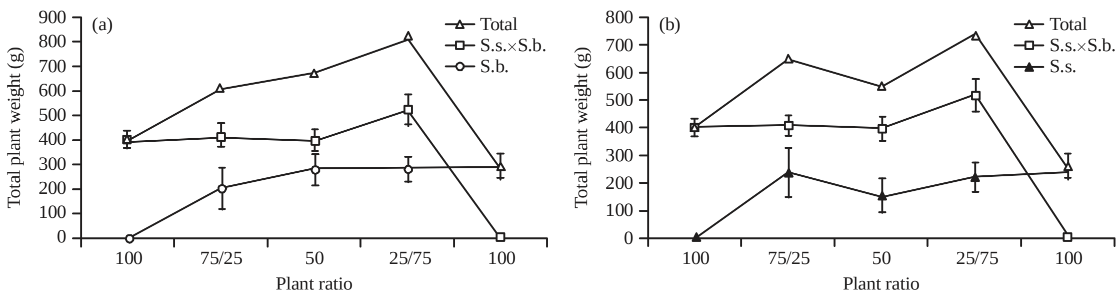

Fig. 10(a-b): Differences on the total plant weight at maturity among *Sorghum sudanense*, *Sorghum bicolor* and their hybrids grown in competition. Bars represent the standard errors

Ratooning showed significant differences among the genotypes with the *S. sudanense*×*S. bicolor* F_1 exhibiting fitness enhancement in monoculture and in plots with mixed plant ratios. In competition with *S. bicolor* the F_1 had an 25:75-hybrid: Crop) (Fig. 5a). Analysis of the number of ratoons showed that the F_1 of *S. halepense*×*S. bicolor* was more competitive than *S. bicolor* parent (intersection after 25:75-F_1: *S. bicolor*) (Fig. 6a). The competitive ability of the F_1 was less pronounced where the *S. halepense*×*S. bicolor* F_1 was grown together with *S. halepense* in competition plots. In this case, the intersection was observed at around 50:50 plant mixture (Fig. 6b). The *S. halepense*×*S. bicolor* F_1 was more competitive than *S. bicolor* on the total number of seed produced per plant. The intersection was seen beyond the 50:50 point (Fig. 7a). Enhanced fitness on seed number was observed in the *S. halepense*×*S. bicolor* F_1. The intersection was towards the 0:100-hybrid:weed crop mixture (Fig. 7b). Enhanced fitness on the F_1 progenies was observed on the total seed weight where the intersection was observed beyond 25:75 in F_1:crop (Fig. 8a) and in F_1:weed plant mixtures (Fig. 8b).

Fitness of *S. bicolor*×*S. sudanense* hybrids grown in the field conditions in competition with their parents: Parental genotypes of *S. sudanense*, *S. bicolor* and the *S. sudanense*×*S. bicolor* F_1 showed significant differences when assayed for reproductive and fitness traits ($p \leq 0.05$) (Fig. 5). Monocultures of the *S. sudanense*×*S. bicolor* (Fig. 9a) had higher number of panicles (5.9) than that of the parental genotypes *S. bicolor* (3) and *S. sudanense* (5). Similarly, *S. sudanense*×*S. bicolor* showed higher fitness under 75:25, 50:50 and 25:75 plant mixtures. The intersection points for both F_1 by crop parent (Fig. 9a) and F_1 by weedy parent (Fig. 9b) were skewed towards 0:100 plant mixtures ratios. The F_1 showed significant fitness than both *S. bicolor* and *S. sudanense* with regard to total plant weight. The intersection was towards 0:100 (F_1: *S. bicolor*) (Fig. 10a) and 0:100-F_1: *S. sudanense* (Fig. 10b) for plant weight.

Ratooning showed significant differences among the genotypes with the *S. sudanense*×*S. bicolor* F_1 exhibiting fitness enhancement in monoculture and in plots with mixed plant ratios. In competition with *S. bicolor* the F_1 had an intersection beyond the 25:75-F_1: crop plant competition mixture (Fig. 11a). A similar situation was observed when the F_1 was planted in competition with the weed (Fig. 11b).

The total numbers of seeds were enhanced in situations where the F_1 was grown in competition mixtures with *S. bicolor* (Fig. 12a) and *S. sudanense* (Fig. 12b). The intersection point in both cases was beyond the 25:75-F_1: Crop and F_1:weed plant competition mixtures. The total seed weight showed significant differences among the genotypes and plant growth mixtures. The F_1 showed enhanced seed weight culminating in intersection points pulled towards the 0:100-F_1:crop (Fig. 13a) and 0:100-F_1:weed (Fig. 13b) plant competition mixtures.

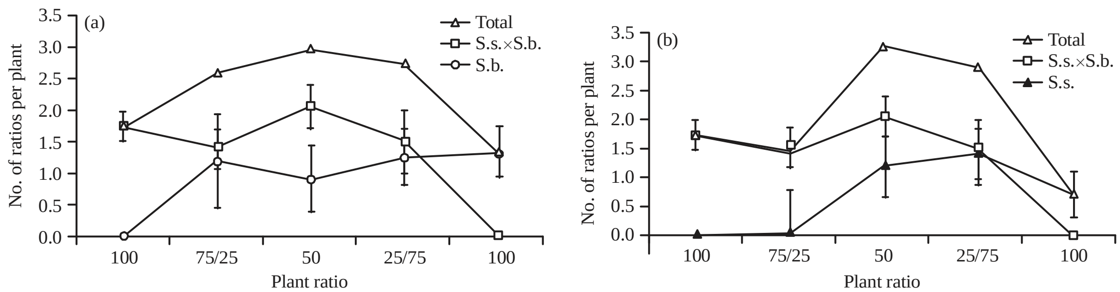

Fig. 11(a-b): Fitness differences on the total number of ratoons per plant among *Sorghum sudanense*, *Sorghum bicolor* and their hybrids grown in competition. Bars represent the standard errors

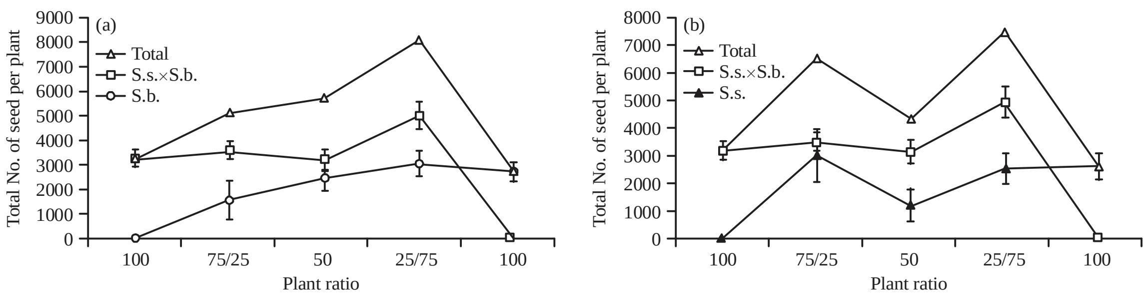

Fig. 12(a-b): Fitness differences on the total number of seeds per plant among *Sorghum sudanense*, *Sorghum bicolor* and their hybrids grown in competition. Bars represent the standard errors

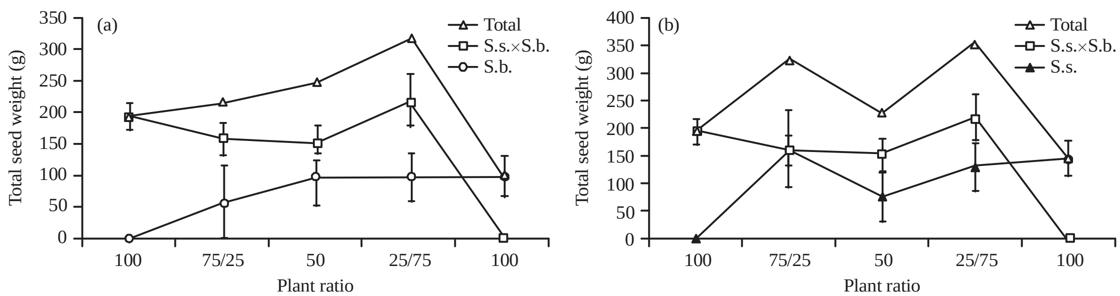

Fig. 13(a-b): Differences on the total seed weight among *Sorghum sudanense*, *Sorghum bicolor* and their hybrids grown in competition. Bars represent the standard errors

Table 2: Relative crowding coefficient values derived from growing parents and their hybrids in varying crop ratios in competition plots

Genotypes	No. of panicles	Plant weight	No. of ratoons	No. of seeds	Seed weight
Sb with (Sh×Sb)	6.2	4.5	5.1	4.3	19.5
Sh with (Sh×Sb)	6.9	27.4	5.0	76.9	5.5
Sb with (Ss×Sb)	10.1	6.7	6.0	6.4	8.6
Ss with (Ss×Sb)	5.2	8.3	34.6	7.0	6.0

Sh: *Sorghum halepense*, Ss: *Sorghum sudanense*, Sb: *Sorghum bicolor*

Relative competitive ability of *S. halepense*×*S. bicolor* and *S. bicolor*×*S. sudanense* hybrids grown in the field in competition with their parents: Relative crowding coefficient of more than 1 showed that the F_1 progenies obtained from hybridizations involving *S. halepense*×*S. bicolor* and *S. sudanense*×*S. bicolor* consistently out performed the parental populations in replacement series assessments (Table 2). Analysis of the number of panicles per plant showed RCC values of 6.2 and 6.9 in competitions between *S. halepense*×*S. bicolor* F_1 by *S. bicolor* the parent and *S. halepense*×*S. bicolor* by the *S. halepense*. Competitions between *S. sudanense*×*S. bicolor* by *S. bicolor* gave a 10.1 value which was larger than all other competitions for the number of panicles (Table 2). Competition between *S. halepense*×*S. bicolor* and *S. halepense* for total plant weight gave a high RCC value (27.4) as compared to the competitions involving the F_1 with *S. bicolor*. Plant competitions with *S. sudanense*×*S. bicolor* had 6.7 and 8.3 RCC values on plant weight. The two F_1 progenies showed high RCC values (above 5) for the number of ratoons when compared to their parents in plant competition mixtures. Competitions involving *S. sudanense*×*S. bicolor* by

Fig. 14: *Sorghum sudanense*×*Sorghum bicolor* hybrids and *Sorghum sudanense* parents grown in the field showing vigour in the F_1

Table 3: *Sorghum halepense*×*Sorghum bicolor* and *Sorghum sudanense*×*Sorghum bicolor* hybrid reproductive features depicting heterosis and improved fecundity in the F_1 progenies

Genotype	No. of panicle	s.e	No. of ratoons	s.e	Total No. of seeds	s.e	Weight seed (g)	s.e	Germination (%)	S.e.d
S. bicolor	1.9	0.2	1.4	0.2	2011.0	168.1	105.1	11.8	87.0	21
S. *halepense*	2.0	0.3	2.9	0.3	1030.0	310.0	77.9	21.9	70.9	21
S. *halepense*×*S. bicolor*	3.3	0.2	1.9	0.2	2436.0	188.0	177.4	13.3	53.0	21
S. sudanense	6.0	0.3	1.5	0.2	2708.0	240.6	129.9	17.0	70.9	21
S. sudanense ×*S. bicolor*	6.3	0.2	1.7	0.2	3520.0	174.3	178.4	12.3	69.6	21

S. sudanense gave a high value 34.6 with regard to the number of ratoons (Table 2). The total number of seeds and total seed weight exhibited high RCC values in all F_1 progenies and weed competitions. High values were seen in the competitions involving *S. halepense*×*S. bicolor* and *S. halepense* (76.9) and *S. halepense*×*S. bicolor* and *S. bicolor* (19.5) (Table 2).

Fecundity of *S. halepense*×*S. bicolor* and *S. sudanense*×*S. bicolor* hybrids grown in the field in competition with their parents: Fecundity was assessed by plant features that enhance the ability of the female parents to produce offspring. Analysis of the number of panicles produced per plant showed that there were differences among the three parents and their hybrids. The *S. sudanense*×*S. bicolor* F_1 had the highest number with 6.3 panicles (Fig. 14), *S. sudanense* had 6 panicles while *S. bicolor* had a mean of 1.9 panicles. The *S. halepense*×*S. bicolor* F_1 had 3.3 panicles as compared to *S. halepense* with 2.0 panicles (Table 3). The number of ratoons produced also differed among the genotypes. There was increase in the number of ratoons from 1.5 in *S. sudanense* to 1.7 in the *S. sudanense*×*S. bicolor* F_1. However, a reduction was observed from 2.9 in *S. halepense* to 1.9 in the *S. halepense*×*S. bicolor* F_1 (Table 3).

The total number of seeds produced in the F_1 progenies exceeded that of each of its respective parents. *S. sudanense*×*S. bicolor* had 3,520 seeds, *S. sudanense* had 2708 seeds while *S. bicolor* had a mean of 2011 seeds. *S. halepense*×*S. bicolor* F_1 progenies produced a mean of 2436 seeds per plant while *S. halepense* had 1030 seed per plant (Table 3). Total seed weight of the genotypes also differed significantly. The F_1 from *S. sudanense*×*S. bicolor* had more seed weight of 178.4 g. *Sorghum bicolor* had 105.1 g while *S. sudanense* had 129.9 g. Similarly the F_1 from *S. halepense* and *S. bicolor* produced a mean of 177.4 g of seed per plant while *S. halepense* produced a mean of 77.9 g. The F_1 progenies had high levels of seed dormancy and poor germination of 53% in *S. halepense*×*S. bicolor* and 69 % in *S. sudanense*×*S. bicolor* even after breaking dormancy.

DISCUSSION

The F_1 progenies obtained from the interspecific crosses showed higher expression in most of the vegetative morphological parameters evaluated in this study. There was significant heterosis on reproductive and vegetative traits in the progenies. The F_1 generation between *S. halepense*×*S. bicolor* had more tillers and branches above the first internode than either of the two parents. The F_1

generation was taller and higher PAR values were observed (Fig. 1). The F_1 flowered earlier with only 86.9% of stems having panicles at maturity. Similarly the F_1 generation between *S. sudanense*×*S. bicolor* had more tillers and flowered earlier than both parents. However the F_1 generation had lower PAR and lesser branches than *S. sudanense* parent. Both interspecific F_1 progenies were heavier than their parents at maturity but had thinner culms than *S. bicolor*. This vegetative vigour was observed throughout growth phase (between day 40-60 to 150) in the F_1 population. The vegetative competitive ability was also enhanced in the F_1 progenies obtained from wide crosses as compared to their parents even when grown in competition (Fig. 2). This drastic increase in vigour could be attributed to heterosis obtained due to hybridization of genetically distant genotypes. The F_1 vigour may not necessarily be due to the presence of crop alleles in the weedy sorghums. Hybrids derived from different species in the same genus have been reported to have greater adaptive advantage due to enhancement of important vegetative features. An F_1 obtained from crossing *O. sativa* and *O. rufipogon* had higher hybrid vigour at the vegetative growth phase and better tillering than the parents (Song *et al*., 2004). In previous results radish F_1 populations showed 27% greater lifetime fecundity and 22% greater survival than wild plants in some environments (Campbell *et al*., 2006).

Higher vigour has also been shown in crop by wild hybrids in lettuce (Hooftman *et al*., 2009). This would result in increasing fitness of their offsprings with regards to their response to drought, salt and nutrient deficiency environments (Uwimana *et al*., 2012). In Gramineae, F_1 hybrids between round-up-ready corn with teosinte showed significantly higher vegetative vigour than that of teosinte (Guadagnuolo *et al*., 2006). F_1 hybrids between crop sorghum and shattercane also exhibited vegetative vigour and higher biomass production as compared to the parents (Sahoo *et al*., 2010). Heterosis seems to be important in F_1 derived from wide crosses in most crop species, with or without presence of robust transgenes, this concurs with results observed in this study.

The F_1 hybrids derived from *S. halepense*×*S. bicolor* and *S. sudanense*×*S. bicolor* exhibited enhanced expression of fitness associated traits while grown in competition. The F_1 population tended to out-crowd the parental genotypes during the growth phase and had more biomass (Fig. 4-8). This led to the increase in the number of panicles, panicle weight and seed number in the F_1 hybrids as compared with their parental populations (Fig. 9-13). The difference between *S. bicolor* and the *S. halepense*×*S. bicolor* F_1 hybrid was minimal with regards to the total number of seeds produced. Underground biomass accumulation also seemed to favour the F_1 progenies resulting in higher ratooning except when *S. halepense* was grown in competition with the *S. halepense*×*S. bicolor* F_1. Ratooning in the F_1 hybrid implies greater proliferation of the F_1 in agricultural systems as volunteer weeds or contaminants in farmers' seed, increasing chances of interspecific hybridization. This would enhance crop allele proliferation and persistence within the weedy background through introgressive backcrossing (Ellstrand, 2003). General vigour in the F_1 enhances the populations' chance to produce more seed and more panicles and therefore fitness. However, fitness of crop×weed hybrids vary across crop species (Ellstrand, 2003) and different agro-ecological environments (Chapman and Burke, 2006). Furthermore, F_1 hybrids did not have significant fitness differences to their parents in maize (Guadagnuolo *et al*., 2006) and shattercane (Sahoo *et al*., 2010). In contrast, crop×wild hybrids in sunflower (Mercer *et al*., 2006) and lettuce F_1 hybrids and backcross populations (Uwimana *et al*., 2012) had higher relative fitness.

The increase in fitness associated traits in F_1 between *S. halepense*×*S. bicolor* and *S. sudanense*×*S. bicolor* differed. The *S. sudanense*×*S. bicolor* F_1 showed more increase on the number of panicles, number of seeds and total seed weight when compared to the parents. The differences in fitness gain or loss among different crop and wild hybrids can be attributed to the different environments of growth and differences in weedy biotypes used in each study. For instance, Arriola and Ellstrand (1997) did not observe any increase in fitness associated trait in the F_1 between *S. halepense* and *S. bicolor*. This could be attributed to the lack of good heterotic combining ability among the biotypes used. Growing the F_1 genotypes being evaluated either in competitive or non-competitive environments may also show some significant effect on the expressed fitness. The intrinsic competitive nature of some plants for example, allelopathy in sorghum may alter the general fitness advantage towards the heterotic $F_{1.}$ Allelopathy is conferred by phytotoxins such as the potent benzoquinone sorgoleone (2-hydroxy-5-methoxy-3-[(Z,Z)-8',11',14'-pentadecatriene]-p-benzoquinone) and its analogs (Baerson *et al*., 2008). Sorgoleone is produced and exuded from root hairs into the soil in such species where it inhibits the growth of other susceptible plants like those belonging to the Stiga species.

In this study, F_1 progenies from interspecific crosses between crop and wild sorghums had higher fecundity accompanied with exaggerated levels of seed dormancy and poor germination (Table 3). The F_1 generation between *S. halepense* and *S. bicolor* had more panicles than both parental genotypes. The second F_1 hybrid between *S. sudanense* and *S. bicolor* was significantly different from *S. bicolor* on the number of panicles but this was not the case when compared with *S. sudanense*. The F_1 had equal or lesser ratoons than its weedy parents, but they had more seed as compared to their parents (Table 3). Germination of the F_1 seed between *S. halepense*×*S. bicolor* (53%) and *S. sudanense*×*S. bicolor* (69.6%) were lower than those of their parents (Table 3). Despite having more seed due to the increase in the number of panicles, the F_1 progenies also had high levels of dormancy. This resulted in poor germination due to rotting of the larger loosely covered endosperm, a characteristic obtained from crop sorghum. Similar results were observed on the seed obtained from the F_1 plants to raise the F_2 population. The results on fecundity have been shown to differ among species with interspecific F_1 and F_3 populations in radish having lower lifetime fecundity (Campbell and Snow, 2007). In addition interspecific hybrids of squash showed lower relative fecundities (Spencer and Snow, 2001). The presence of crop sorghum alleles in *S. halepense* populations (Morrell *et al*., 2005) show that reduced fitness and fecundity in some crop to wild crosses may not defer the proliferation and persistence of crop alleles in weedy backgrounds. The F_1 population does not represent a barrier to introgression of neutral, null or beneficial alleles into weeds or wild sorghum populations.

CONCLUSION

The F_1 progeny obtained from the interspecific crosses showed higher expression at most vegetative morphological parameters evaluated in this study. This drastic increase in vegetative vigour could be attributed to heterosis obtained due to hybridization of genetically distant genotypes. Fitness associated traits of F_1 hybrids derived from *S. halepense*×*S. bicolor* and *S. sudanense*×*S. bicolor* grown in competition with their parents were enhanced. All, the F_1 progenies had equal or lesser ratoons than the weedy parents but they had more seed as compared to their parents. All the F_1 populations had exaggerated levels of seed dormancy and forced germination of the F_1 seed gave 53% in *S. halepense*×*S. bicolor* and 69% in *S. sudanense*×*S. bicolor* which were lower than those of their parents. This study is especially important due to maintenance of genes that boost agronomic performance in crop species that grow in sympatry with their wild progenitors harbouring weedy traits.

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