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BRIEF REPORT

Maternal effects in Gadam and high-tannin sorghum varietal crosses

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Abstract Maternal effects on agronomic traits in sorghum hybrids were studied through reciprocal crosses of Gadam with Serena, Seredo, and KARI Mtama 1. Reciprocal hybrids Serena x Gadam, KARI Mtama 1 × Gadam, and Seredo x Gadam were 9, 17, and 21 cm taller than their direct crosses.Query Reciprocal crossing delayed heading by 10, 8, and 14 days; flowering by 8, 6, and 16 days; and maturity by 16, 8, and 4 days in Serena x Gadam, Seredo x Gadam, and KARI Mtama 1 × Gadam, respectively. The hybrids also differed significantly in grain-filling percentage. These results emphasize the extent and direction of maternal effects on sorghum agronomic traits.

Keywords Agronomic traits · Hybrids · Reciprocal crosses

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Introduction

Plant breeders evaluate extranuclear influences, especially maternal effects in seeds, through reciprocal crosses (Tariba 2023). According to Holeski et al. (2012) and Herman and Sultan (2011), maternal effects are transgenerational forms of phenotypic plasticity transmitted from the maternal parent in response to environmental conditions, rather than DNA sequence changes. Environmental stimuli experienced by the mother plant can cause modifications that later appear in the offspring (Jablonka and Raz 2009). These effects impact offspring development, fitness, and resistance to biotic stress, especially pests (Vivas et al. 2019).

Selection response in the presence of maternal effects is influenced by both direct and indirect genetic effects, leading to outcomes that may be dampened, accelerated, or even counterintuitive (Hoyle and Ezard 2012; Wolf and Wade 2016). Controlled breeding under field and greenhouse conditions shows that these indirect effects can either limit or amplify selection (Bijma 2014; Marjanovic et al. 2022). Maternal effects are transmitted via two non-exclusive pathways: seed provisioning and epigenetic inheritance (Herman and Sultan 2011). Seed provisioning involves the maternal transfer of nutrients and somatic resources and is restricted to a single generation (Elwell et al. 2011). Epigenetic transmission includes histone modifications, DNA methylation, and small RNAs that can be inherited across

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multiple generations (Brautigam et al. 2013; Hauser et al. 2011).

This paper reports maternal effects on agronomic traits in F_1 sorghum hybrids produced by crossing Gadam cultivar with high-tannin varieties. These specific varietal combinations between Gadam and high-tannin sorghum have not been previously evaluated for trait-specific maternal effects. The study thus provides new insights into how maternal influences affect agronomic traits, including days to heading, plant height, flowering, grain filling and maturity in these hybrid crosses.

Materials and methods

The experiment was conducted at the University of Embu research farm, which is characterized by *Humic nitisols*. The study site is situated at an altitude of 1463 m above sea level, receiving about 1230 mm of average annual rainfall, with a mean yearly temperature of 19.6 °C (Jaetzold et al. 2007). Seeds of four sorghum varieties, Gadam, KARI Mtama 1, Seredo, and Serena, were sourced from the Kenya Agricultural and Livestock Research Organization (KALRO). Gadam is an early-maturing, low-tannin sorghum variety, while Serena and Seredo are late-maturing, high-tannin varieties. KARI Mtama 1 is a white-grained sorghum used as a control in the study. The varieties differ in their heading times of approximately 45, 58, 71, and 70 days for Gadam, KARI Mtama 1, Serena, and Seredo, respectively. These contrasting traits provide a suitable basis for evaluating maternal effects in the crosses.

The field trials adhered to a Randomized Complete Block Design with three replications, involving ten treatments, including direct and reciprocal hybrids and their parental varieties. Flowering was synchronized by sowing donor parents (KARI Mtama 1, Serena, and Seredo) in advance, followed by the recipient parent (Gadam) in three staggered batches at weekly intervals (7-day intervals) to ensure overlapping flowering for direct crosses. For reciprocal crosses, roles were reversed, with Gadam as the donor and the other varieties as recipients, maintaining staggered sowing to synchronize flowering. Crosses were performed at panicle emergence using manual emasculation and artificial pollination (Shinda et al. 2021) to produce the F_1 hybrids and their reciprocals.

Standard agronomic practices (Bonin et al. 2016; Hanway and Olson 2012; Thivierge et al. 2015), were followed, including fertilizer application (TSP and CAN), weeding, and pest control. Before flowering, five plants were randomly tagged from the middle rows of each treatment for data collection on grain-filling percentage, plant height, days to heading, flowering, and maturity. Data were analyzed using one-way ANOVA in R statistical software (R Development Core Team 2015), and mean separation was performed using Tukey's Studentized Range (HSD) test at 95% confidence with the agricolae package (De Mendiburu 2019).

Results

While earlier studies mainly examined compatibility and heterosis (Shinda et al. 2021), this research provides new evidence on the extent and direction of maternal effects influencing agronomic traits in sorghum (Table 1). Parental varieties, as well as direct and reciprocal crosses, differed significantly ($p < 0.001$) across all measured traits. Gadam exhibited the shortest average plant height (103.3 cm) compared to Serena (144.7 cm), Seredo (151.0 cm), and KARI Mtama 1 (170.3 cm), notably impacting the plant height of the direct hybrids, which were generally shorter than their parents and reciprocal crosses. The direct crosses of Gadam with Serena, Seredo, and KARI Mtama-1 recorded plant heights of 99.5, 127.1, and 142.3 cm, respectively, significantly lower than their reciprocal crosses, which measured 120.4, 136.0, and 159.5 cm, respectively. Significant differences were also observed for days to heading, flowering, and maturity among parents and hybrids. Gadam had fewer days to heading (55.7 days) compared to KARI Mtama 1, Serena, and Seredo, which recorded 61.6, 65.1, and 68.6 days, respectively. The direct crosses Gadam x KARI Mtama 1, Gadam x Serena, and Gadam x Seredo showed significantly fewer days to heading (43.8, 53.8, and 56.3 days) compared to their reciprocal crosses, which had 58.1, 63.7, and 64.0 days, respectively.

Gadam sorghum portrayed an early flowering and maturity of 65.3 and 97.7 days, followed by KARI Mtama 1 with 70.2 and 99.4 days to flowering and maturity, respectively. Serena flowered and matured

Table 1 Maternal effects on growth and yield traits in sorghum direct and reciprocal crosses

Parent/ Crosses	Entry (♀ x ♂)	Plant height (cm) (Mean ± S.E)	Days to heading(Mean ± S.E)	Days to flowering(Mean ± S.E)	Days to maturity(Mean ± S.E)	% Grain filling (Mean ± S.E)
Parents	Gadam	$103.287^{f} \pm 4.181$	$55.733^{de} \pm 0.371$	$65.267^{ef} \pm 0.267$	$97.667^{de} \pm 0.267$	$98.519^{a} \pm 0.098$
	Serena	$144.747^{bcd} \pm 2.177$	$65.067^{ab} \pm 0.521$	$74.533^{a} \pm 0.371$	$109.867^{b} \pm 1.593$	$98.275^{ab} \pm 0.101$
	Seredo	$151.007^{abc} \pm 0.903$	$68.600^{a} \pm 1.206$	$75.867^{a} \pm 0.581$	$116.753^{a} \pm 1.888$	$98.485^{a} \pm 0.107$
	KARI Mtama 1	$170.347^{a} \pm 2.864$	$61.600^{bc} \pm 0.115$	$70.200^{cd} \pm 0.917$	$99.400^{cde} \pm 1.311$	$97.914^{bc} \pm 0.163$
Direct crosses	Gadam x Serena	$99.480^{f} \pm 2.212$	$53.800^{e} \pm 0.400$	$63.200^{f} \pm 0.416$	$87.000^{f} \pm 0.987$	$97.195^{de} \pm 0.107$
	Gadam x Seredo	$127.127^{de} \pm 6.484$	$56.333^{de} \pm 0.133$	$66.967^{e} \pm 0.418$	$96.200^{e} \pm 1.114$	$96.789^{e} \pm 0.100$
	Gadam x KARI Mtama 1	$142.293^{bcde} \pm 2.775$	$43.800^{f} \pm 1.331$	$52.200^{g} \pm 0.529$	$93.600^{e} \pm 1.026$	$98.177^{ab} \pm 0.095$
Reciprocal crosses	Serena x Gadam	$120.473^{ef} \pm 7.101$	$63.733^{b} \pm 0.333$	$71.400^{bc} \pm 0.231$	$103.267^{cd} \pm 1.157$	$98.399^{a} \pm 0.077$
	Seredo x Gadam	$136.013^{cde} \pm 6.608$	$64.000^{b} \pm 1.249$	$73.400^{ab} \pm 1.102$	$104.667^{bc} \pm 1.622$	$97.569^{cd} \pm 0.064$
	KARI Mtama 1×Gadam	$159.473^{ab} \pm 5.591$	$58.133^{cd} \pm 0.371$	$67.933^{de} \pm 0.067$	$97.933^{de} \pm 0.481$	$96.175^{f} \pm 0.114$
P – Value		< 0.001***	< 0.001***	< 0.001***	< 0.001***	< 0.001***

Means with the same letter within the column are not significantly different. *** significant at 0.1%. S.E.-standard error; %-percent; cm-centimeters; ♀ Female or recipient parent; ♂ Male or donor parent. Plant height was measured at the active vegetative stage

in 74.5 and 109.9 days while Seredo flowered and matured in 75.9 and 116.8 days respectively. Direct crosses of Gadam x KARI Mtama 1, Gadam x Serena, and Gadam x Seredo flowered at 52.2, 63.2, and 67.0 days, which was significantly earlier than their reciprocal crosses, which flowered at 68.0, 71.4, and 73.4 days. For days to maturity, Gadam x KARI Mtama 1, Gadam x Serena, and Gadam x Seredo matured significantly earlier at 93.6, 87.0, and 96.2 days, respectively compared to their reciprocal crosses, which matured at 97.9, 103.3, and 104.7 days. Gadam recorded a grain filling percentage of 98.52%, similar to Serena (98.28%) and Seredo (98.49%), but significantly higher than KARI Mtama 1 (97.91%). The direct crosses of Gadam x KARI Mtama 1, Gadam x Serena, and Gadam x Seredo had grain filling percentages of 98.1, 97.2, and 96.8%, respectively, and these differed significantly—but with no trend—from their reciprocal crosses, which recorded means of 96.2, 98.4, and 97.6%, respectively.

Discussion

Plant breeders often use reciprocal crosses to detect variation associated with outbreeding depression or maternal inheritance, as parents with different cytoplasmic backgrounds can produce reciprocal hybrids that differ in measurable traits (Gai and He 2013). Maternal effects have been noted in many crops and across various agronomic traits, and understanding these influences helps breeders select parents that enhance trait expression in the next generation (Beyene et al. 2016). Therefore, reciprocal crosses are a vital method for determining whether a trait is affected by maternal inheritance, although the extent of these effects can vary among traits. For instance, Liu et al. (2016) demonstrated that the inheritance of certain traits in Pyrus depends on whether a cultivar is used as the female or male parent.

In this study, taller maternal parents (Serena, Seredo, and KARI Mtama 1) produced taller hybrids in reciprocal crosses, while using the shorter Gadam as the maternal parent resulted in reduced plant

height in the progeny. This consistent link between hybrid height and the maternal parent indicates that variations in plant height are mainly affected by maternal or cytoplasmic effects. These findings agree with Guden and Uzun (2024), who, while examining heterosis in biomass-related traits in sorghum F_1 reciprocal hybrids, reported that the reciprocal cross effect significantly influences the inheritance of plant height. Mohammed et al. (2016) observed notable reciprocal differences for shoot-fly resistance in sorghum, attributed to cytoplasmic factors. Similar effects have also been shown to influence the inheritance of plant height, as well as traits such as tassel length, ear height, and leaf area in maize improvement (Calugar and Rotar 2016).

Hybrids with Gadam as the maternal parent showed early heading, flowering, and maturity, whereas when the longer-duration parents (Serena, Seredo, and KARI Mtama 1) served as maternal parents, the hybrids exhibited delayed heading, flowering, and maturity. These reciprocal differences provide strong evidence of maternal effects, particularly highlighting the influence of cytoplasmic inheritance on these traits. The observed patterns can be attributed to genes located in organelles such as mitochondria or chloroplasts, which are transmitted exclusively through the maternal line (Greiner et al. 2015). This aligns with the observations of Chhagan (2021) and Mohammed et al. (2015), who reported that maternal effects in grain sorghum significantly affected the inheritance of both agronomic and morphological traits. These findings are also consistent with those of Roy et al. (2010), who identified significant maternal effects for these traits in rice. Similarly, Owusu et al. (2020) reported large reciprocal effects in cowpea, indicating that maternal or cytoplasmic influences are important.

Although statistically significant differences in grain filling percentage were observed between direct and reciprocal crosses, the magnitude of these differences was small and lacked a consistent directional pattern. The plausible explanation is that grain filling in sorghum is marginally influenced by maternal or cytoplasmic inheritance but predominantly determined by nuclear genetic factors and environmental conditions. This observation may have practical implications for sorghum breeding programs aiming to combine the improvement of developmental and phenological traits with grain filling efficiency and yield which is a popular breeding objective. These findings differ with Tao et al. (2011) who reported significant cytoplasmic effects for filled-grain ratio in *indica* rice. Maternal effects have recently been documented in rice for heterosis and quality-related traits through hybrid performance (Gu and Han 2024; Manlulu et al. 2025), as well as reciprocal differences in yield traits including grain weight and panicle number (Harijan et al. 2021).

The study was limited by the small number of parental lines which may restrict the generalizability of the findings across broader sorghum germplasm yet maternal effects are genotype dependent. Due to lack of adequate resources, the study applied an incomplete diallel crossing design which denied the opportunity to assess the general and specific combining abilities alongside maternal effects. In addition, the study was conducted under a single environmental condition, thereby constraining the assessment of genotype-by-environment interactions which may possibly modify the maternal effects on phenological and yield traits.

Conclusion

This study demonstrated significant maternal (cytoplasmic) effects in sorghum, for plant height, days to heading, flowering, and maturity. However, maternal effects on grain filling percentage were found to be weak and inconsistent indicating that this trait may be predominantly governed by nuclear genetic factors and environmental conditions rather than maternal or cytoplasmic inheritance. The novelty of this research lies in demonstrating trait-specific maternal effects in commonly used sorghum varieties in Kenya. The strong association of maternal effects with developmental and phenological traits and their apparent limited role in grain filling offers a new insight into the genetic control of yield components. These findings are practically useful to plant breeders for designing an efficient crossing pattern in hybrid development programs for sorghum especially in marginal areas where early maturity and efficient grain filling are needed.

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Data availability The data supporting the findings of this study are available from the corresponding author upon request.

Declarations

Conflict of interest The authors declare no competing interests.

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