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FEASIBILITY OF BASMATI HYBRID SEED PRODUCTI ON IN KENYA USING HIGH-TEMPERATURE–INDUCED EGMS (2-LINE SYSTEM)

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ABSTRACT

The need to increase rice yield has prompted breeders to adopt hybrid rice seed technology. The main challenge has been finding a female parent that is completely male-sterile so it can be pollinated by a pollen donor. Basmati rice lines are difficult to cross with other lines, limiting the use of their hybrids for yield improvement. The objective of this study was to cross Environment-Sensitive Genic Male Sterile (EGMS) with Basmati to produce hybrid Basmati rice seeds to improve rice yield in Kenya. Photoperiod-sensitive genic male-sterile rice lines IR-73827-23-76-15-7 S and IR-75589-31-27-8-33-2S, and a thermosensitive genic male-sterile line, IR-77271-42-25-4-36S, known as P1, P2 and T1, respectively, were obtained from the International Rice Research Institute. These lines were grown under greenhouse (GH) conditions, where temperatures exceeded 34°C to induce complete male sterility. Results showed that under high GH temperatures, both PGMS and TGMS lines had over 89.2±1.8ef pollen sterility, which positively corresponded with over 98.9±0.3d spikelet sterility, whereas Basmati (370 and 217) had as low as 85.8±2e pollen sterility and 69.5±1.1c spikelet sterility, particularly for Basmati217. The best hybrid seed yield was from the cross between Basmati217 and T1(V3), with an average of 39.12%, compared to the control lines (unpollinated), which had 0% seed production, indicating the potential for local Basmati seed production. When tested under GH growth conditions, hybrid lines P1B217 and P2B217 had the highest filled spikelet of 68.5±1.2e and 69.5±1.4e, compared to Basmati370 and 217, which had 37.1±1.4b and 34.3±1.3b, and EGMS P1 and T, which had filled spikelets of 0.7±0.3a and 1.7±0.4a, respectively. This indicates the feasibility of increasing Basmati yield in Kenya using hybrid seed technology (EGMS method) with hybrid seeds free of contamination from self-bred seeds. Additionally, Basmati370 appears to exhibit better heterosis than Basmati217 for most strains studied. In conclusion, the EGMS method should be enhanced to produce Basmati hybrid rice seeds to increase yield and food security.

Key words: Basmati, EGMS, Hybrid Rice, Greenhouse, Male-Gamete, Sterility, *Oryza sativa*

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INTRODUCTION

Rice is a monocot plant and a member of the grass family Gramineae, belonging to the genus Oryza. The genus comprises 25 species that grow in tropical and subtropical regions. Among these species, only Oryza sativa L. and Oryza glaberrima Steud. are cultivated [1]. There are three recognised subspecies of O. sativa: japonica, indica, and javanica [2]. Together, these three subspecies account for the bulk of cultivated rice, the third most important food crop globally, after maize and wheat. In 2023, global paddy rice production was estimated at 518.1 million metric tonnes [3]. In recent years, rice utilisation has increased, while production has grown only slowly.

Many consumers prefer basmati rice to non-aromatic varieties for its aroma and cooking qualities [4]. Unfortunately, basmati yields per hectare are lower than those of non-aromatic lines [5], keeping prices high. Basmati 370 and 217 are the two major aromatic rice varieties grown in Kenya. They account for 98.8% of the total rice grown by farmers in the Mwea Irrigation Scheme, Kenya's main basmati rice-producing region. In 2023, Kenya's total rice consumption was over 1166.2 tonnes, while the Kenya National Bureau of Statistics 2024 indicate a total yield of about 229.06 tonnes, with an average of 3.6 to 4.0 tonnes per hectare [6]. The deficit of over 937.1 metric tonnes was met by imports in 2023 [7, 8]. Therefore, Kenya needs a rice production strategy to offset the burden of imports.

The green revolution of the 1960s and 1970s introduced the semi-dwarf (sd1) gene into rice and wheat, transforming them from tall to short stature [9]. Plant varieties with the semidwarfing allele sd-1 tolerate higher doses of nitrogenous fertiliser than tall varieties, significantly increasing yields [10]. However, by the 1980s and 1990s, the high-yielding varieties produced by the green revolution had reached a breeding plateau [11]. Fortunately, “super-yielding hybrid rice” technology was discovered, which could break the plateau. This further increased rice yield by an average of 20-30% over pure-bred lines [12,13]. Common methods in hybrid rice production include the three-line system, which utilises cytoplasmic male sterility (CMS) [14], and the two-line hybrid system, referred to as environment-sensitive genic male sterility (EGMS) [15-17]. Among the EGMS, the photoperiod-sensitive genic male-sterile (PGMS) rice line is completely sterile under 14 hours of daylight and reverts to varying degrees of fertility under less than 14 hours [15, 16]. The other EGMS is a thermosensitive genic male-sterile (TGMS) rice line that is sterile under high-temperature conditions and reverts to some fertility under low-temperature conditions [18]. In their sterile phase, the EGMS rice lines are crossed with a male parent to produce F1 (hybrid) seeds [19, 20].

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Kenya needs to adopt a hybrid rice production programme to improve local yields, particularly for basmati, whose consumer preference has driven demand far above supply. Current data show that Kenya imports 90% of its rice consumption [21]. Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA)-based studies indicate that increasing local rice production would reduce imports and increase employment in the milling industry [21]. To realise this goal, Kenya intends to raise local rice production from 156,000 MT in 2018 to 1,301,000 MT in 2030 [22]. This research tested the suitability of using EGMS lines to develop basmati hybrid rice lines by crossing EGMS (PGMS and TGMS) with basmati (B370 and B217) under greenhouse conditions in Mwea, to produce basmati hybrid seed that, in turn, will increase rice yield and overall food security. Using EGMS to produce hybrid rice is less expensive than using the cytoplasmic sterility system because it involves two parents (a male gamete-sterile parent and a pollinator). In comparison, CMS uses three parents (Male gamete sterile parent, maintainer, and Resorer) [13]. This makes it a cost-effective method of hybrid seed production. Hybrid intersubspecies indica/japonica hybrids have been reported to be better than intraspecific indica/indica, which is better than intraspecific japonica/japonica, with about 30% compared to pure-bred rice lines [16].

In Kenya, Specific Combining Ability (SCA) of F1 generations from crosses of Dourado x Nerica 3 and Mwur 4 x Nerica 3 indicates improvement in grain yield and other yield-defining parameters [23]. Evaluation of F2.3 generations of the Nericas and Basmati-370 has indicated the potential to improve rice yield and quality through hybridisation [23]. However, this initiative would be possible only if a programme of hybrid seed development were available.

Cytoplasmic male sterility (CMS) and environment-sensitive genic male sterility (EGMS) are the two main systems used to produce seed for farmers [15]. This study is testing and introducing EGMS seed production in Kenya. Figure 1 below illustrates hybrid rice production using the 2-line (EGMS) system compared with the 3-line (CMS) system. In the 2-line system, the seed multiplication stage in step 1 is achieved through self-pollination by growing the EGMS under a fertility-inducing environment [20]; however, in the 3-line system, a maintainer line is crossed with CMS to obtain seeds for the next generation. This makes the EGMS (2-line system) less expensive to use for producing hybrid seeds, which is why the technology is being tested for adoption in Kenya.

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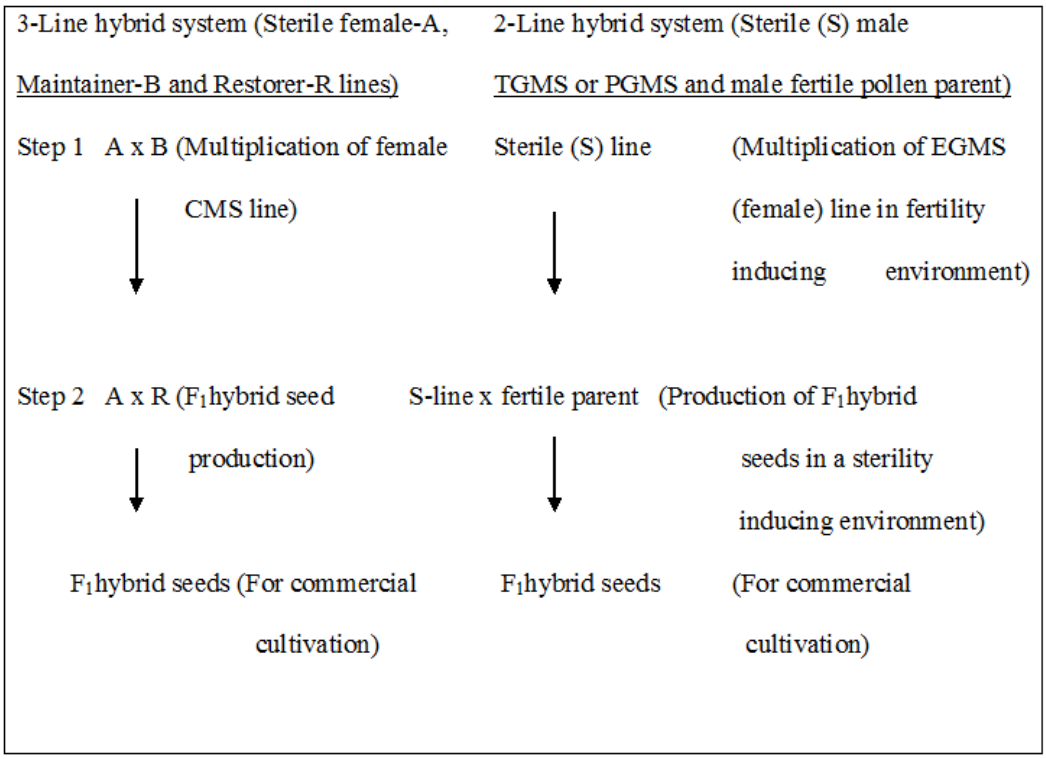

Figure 1: Schematic representation of a 2-line system and a 3-line system of producing hybrid rice [24]. CMS = Cytoplasmic male sterility, while EGMS = Environment

Genic Male Sterile

Past hybrid rice research has focused on producing a P/TGMS basmati and on restructuring basmati stature to improve yield, including breeding a dwarf basmati rice [25]. However, studgy forms the basis of hybrid basmati seed production in Kenya.

MATERIALS AND METHODS

Materials

Environmental genic male-sterile (EGMS) rice varieties, used as female (♀) parents, were IR-73827-23-76-15-7S (P1) and IR-75589-31-27-8-33S (P2), both photoperiod-sensitive genic male-sterile (PGM) lines, and IR-77271-42-5-4-36S (T), a thermosensitive genic male-sterile (TGMS) line. All were imported from IRRI (Philippines) in accordance with the Kenya Plant Health Inspectorate Service (KEPHIS) importation rules and regulations. The male parents (♂), B370 and B217, were provided by the Mwea Irrigation Agriculture (MIAD) centre of the National Irrigation Board (NIB). Sowing was carried out at KARLO-Mwea in Kirinyaga County, Central Province, Kenya. The site is at Latitude 0.7°S and Longitude 37.37E, where day and night lengths are nearly equal. Here, short-day length is 12 hours of daylight.

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Research Methods

Sowing and testing for the adaptability of EGMS lines

The EGMS lines, PGMS line one (P1), PGMS line two (P2), and TGMS (T), along with basmati rice seeds, were placed separately in germinating bags and submerged in 2% H2O2 for 72 hours to break seed dormancy, with a fresh H2O2 solution changed after 24 hours.

Figure 2: Illustration of the parents used in this study, where Parent 1(P1=V1), Parent 2 (P2)=V2 and Parent 3 (P3)=V3. The EGMS parents were grown under h

They were sown on germination plates in a nursery and grown for 21 days. Seedlings were transplanted at 20 cm × 20 cm spacing in concrete-block troughs in the greenhouse (GH). Basmati seedlings were grown both inside and outside the GH, alongside EGMS as negative and positive controls, respectively. The temperature in the GH was maintained above 35°C during the day and at 20°C at night. To achieve this, the GH was calibrated by monitoring dairy temperature and opening and closing it to achieve optimum temperatures, not higher than the maximum of 40°C. Temperature-induced heat stress results in physiological damage to growth [26].

Screening for male sterility

During the first 10 days after flowering, 10 plants per variety were selected, and pollen samples were taken every two days for pollen sterility testing. Samples from B370 and B217 were used as controls. Three unhisened spikelets (from top, middle and bottom) from one panicle per plant were randomly selected from plants in the GH and outside the GH. They were fixed in 70% alcohol. Three anthers from each spikelet were stained by placing an anther on a drop of 1% I2KI (iodine potassium iodine) on a glass slide, then macerated with forceps to release pollen, followed by

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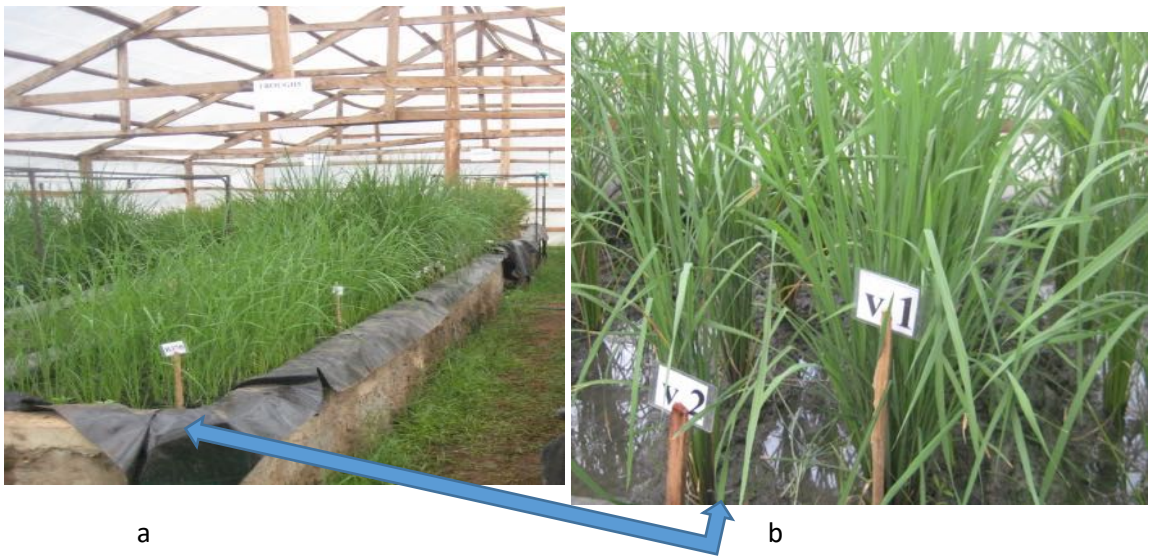
observations under an X10 objective of a light microscope. Pollen fertility was determined by counting ≥50 sterile/abortive (yellow and brown-stained) against fertile (dark blue-stained) randomly observed pollen cells. The % fertile pollen (at heading) and fertile spikelets (at maturity) in plants were calculated using the equations below [17];

$$Pollen\ sterility(\%) = \frac{Total\ number\ of\ sterile\ pollen\ grains}{Total\ number\ of\ pollen\ grains\ in\ (fertile+unfertile)} X100 \qquad \text{Equation 1}$$

$$Spikelet\ fertility(\%) = \frac{Total\ number\ of\ filled\ grains}{Total\ number\ of\ spikelets\ in\ (filled+unfilled)} X100 \qquad \text{Equation 2}$$

Production of hybrid rice

The following crosses were made: P1 X B370, T X B370, P2 X B370, P1 X B217, T X B217 and P2 X B217. These were produced by crossing EGMS (♀) with Basmati (♂) to obtain F1 hybrids. Pollen donors were sown outside the GH, while female plants (P1, P2 and T) were grown under GH conditions. Sowing was staggered in three stages (as part of the ongoing Basmati super hybrid research project, which began with the first planting on September 23rd, 2012) to ensure synchrony between the pollen donor and its recipient.



a b

Figures 3a & b: EGMS gown in greenhouse and in a second stager. These are the ones given high temperature treatment and pollinated with basmati pollen donors grown outside the greenhouse

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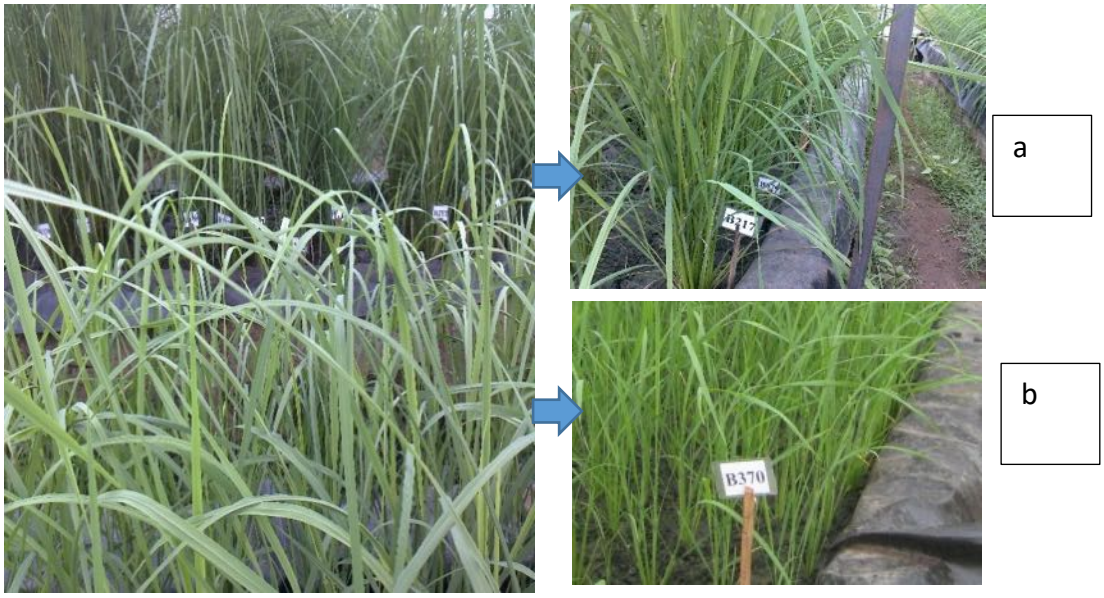

Figure 4: Basmati (370 and 217) pollen donors: Basmati was sown at different times to ensure that when the EGMS in Figure flowers, pollen is always available for pollination. Figure a shows the first sowing, and Figure b shows the 3rd staggered sowing

The first objective was to develop a synchronised system so that, when the EGMS (female parent head) is in flower, pollen is available for cross-pollination. This was achieved by sowing in stages. In stage 1, only basmati 370 and 217 pollen donors were sown, so that, if the EGMS are early-flowering, they will catch up with the earlier-sown BS370 & 217; in stage 2 (10 days after stage 1), B370, B217 and EGMS lines (P1, P2, and T) were sown; and in stage 3 (20 days after stage 1), only lines B370 and B217 (pollen donors) were sown. At the Critical sterility point (CRP), which is 30 days before heading, the EGMS and basmati (Ck) parents were exposed to high temperature under GH growth conditions until heading, when female plants were pollinated with pollen from male parents. Glumes were clipped at the tips to expose the stigma, and pollen from fertile B370 and B217 was dusted over the clipped tips between 12.30 pm and 1.30 pm. Pollinated panicles were then bagged to prevent unwanted crossings.

Evaluation of Agronomic Traits

Hybrids and parental lines were planted in a randomised complete block design (RCBD) with three replicates (Figure 6). This was duplicated three times. In each block, an agrochemical was applied to control insect pests and diseases. Morphological traits were measured at physiological maturity, including plant height and the number of effective tillers. Other evaluated characteristics included days to full maturity and dry grain weight. Plant height was measured in centimetres from the base to the tip of the tallest leaf or panicle, whichever was longer. Effective tillers

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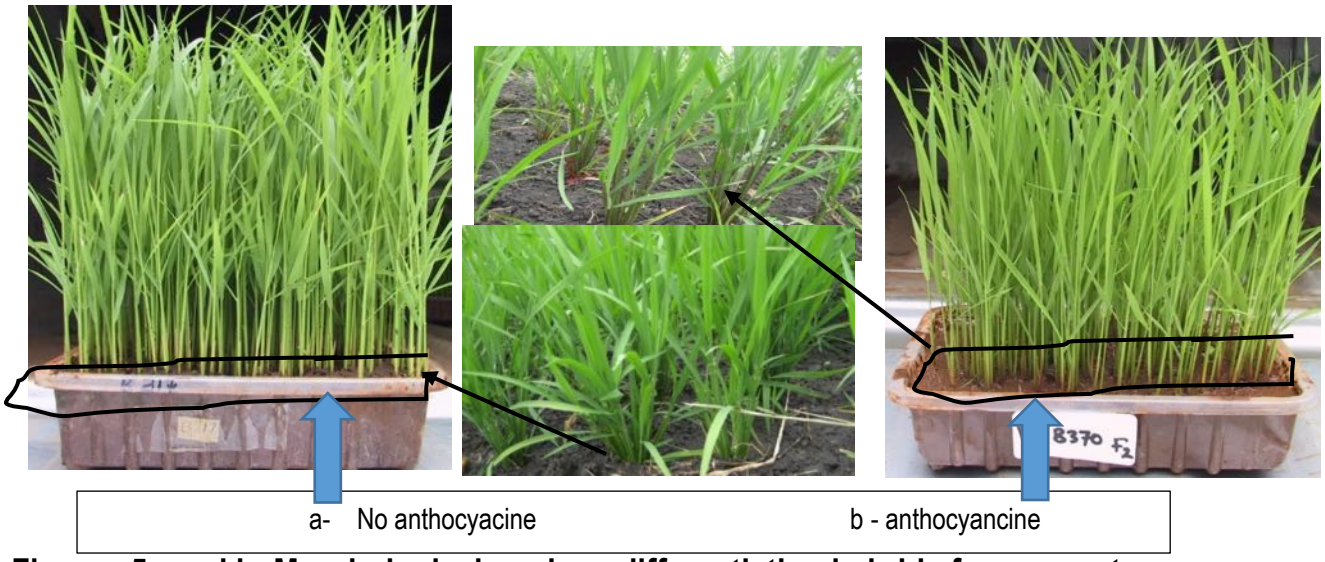
for each sampled plant were counted to determine the total number of panicles. An average of three randomly selected panicles per plant was measured, and the number of glumes was counted [17]. Seeds from each plant were bulked, counted with a seed counter after harvest, and the 1000-seed weight in grams was calculated for each genotype. Days to heading were recorded at 50% panicle emergence from sowing, while days to maturity were noted 30 days after 50% flowering.



Figures 5a and b: Morphological markers differentiating hybrids from parents

The percentage (%) seed set was determined as: (total number of filled grains/total number of spikelets) × 100. Also, 1000-seed weight per variety was evaluated. Hybrids were identified by the presence of anthocyanin in the plant stem. whereas the parents did not.

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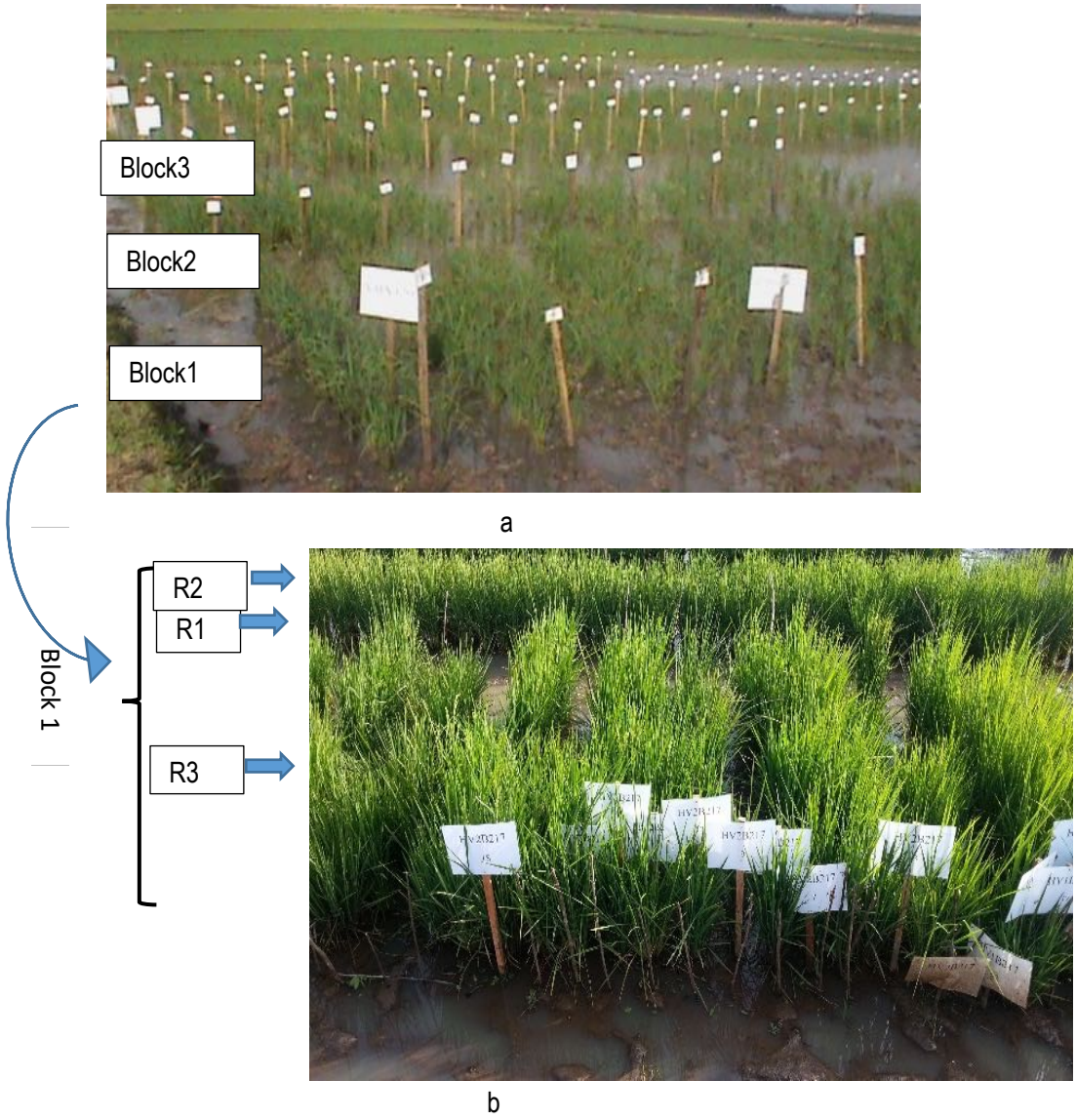

Figures 6a & b: Experimental design - randomised complete block design (RCBD) to test the performance of various hybrids. Figure a illustrates the blocks, each block has been replicated as explained in Figure b, where R = replicate

Data analysis

Data on temperature, parental pollen viability, height, productive tillers, flowering date, seed setting, panicle length and exertion were analysed using ANOVA in SPSS 30.0 [27]. Numerical data from two environments were expressed as mean±SD and analysed using Student's t-test for significance. At $p \leq 0.05$, mean values were considered statistically significant.

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RESULTS AND DISCUSSION

Sterility in EGMS varieties under GH growth conditions

Under GH growth conditions, temperatures averaged about 24˚C and 34˚C, respectively. Under GH growth conditions, lines P1, T, and P2 recorded pollen fertility of less than 2%, while B217 and B370 recorded 25% and 21%, respectively. All lines grown under OGH conditions exhibited pollen fertility over 60% (Figure 7).

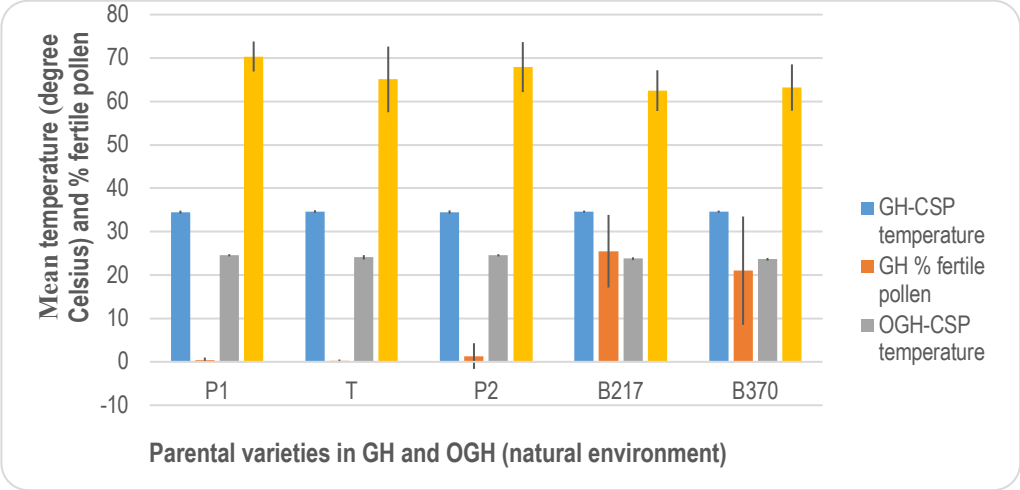

Figure 7: Pollen sterility and fertility inside and outside greenhouse growth conditions. GH=Greenhouse; OGH=Outside greenhouse; CSP=Critical sterility points

Pollen fertility under GH and OGH growth conditions

Temperatures were measured in degrees Celsius, and pollen fertility is expressed as a percentage. Lines P1 and P2 denote PGMS, line T denotes TGMS, and B denotes Basmati.

Figure 7 illustrates the relationship between temperature, EGMS, and Basmati parents. Environment-sensitive genic male sterile (EGMS) rice grown at temperatures above 34°C in the greenhouse showed over 98% of pollen staining yellow with 1% potassium iodide (1% KI) (Figure 7). This indicates that the pollen was sterile [28] and therefore could not be used for fertilisation to produce seeds. However, pollen from Basmati217 and 370 had over 20% staining blue-black, suggesting that greenhouse conditions could induce complete male gamete sterility in the EGMS (PGMS and TGMS) rice lines but not in non-EGMS lines. PGMS are male gamete-sterile when grown under long-day conditions (more than 13.5 hours of daylight) [28]. In this study, they were cultivated under greenhouse conditions with a 12-hour photoperiod, and over 98% stained yellow, indicating sterility. Therefore, high temperature appears to have compensated for the long day length typically required to induce complete pollen sterility in PGMS lines P1 and P2. Even in

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temperate regions, high temperatures reduce the photoperiod needed to trigger complete male sterility in PGMS [29].

Pollen fertility for EGMS lines under GH growth conditions ranged from 0 to 1%, whereas for the controls, B217 and B370 grown under the same GH environment, it was 25% and 20%, respectively (Figure 7). Therefore, a temperature of 34 °C or higher fully induced male sterility in P1, P2, and T, but not in B217 and B370. The sterile pollen stained yellow or faded blue-black with 1% KI (Figure 7d). The results of EGMS grown under GH conditions for emasculation of male gametes using high temperature (HT) and under outside greenhouse growth conditions subjected to an unpaired t-test analysis are shown in Table 2. Line P1, with 2.4×10^{-11}, had the highest pollen sterility rate compared to Basmati 370, with 5.6×10^{-12} sterility levels when grown under GH conditions. On the other hand, P1, with 6.9×10^{-11}, had the lowest fertility levels among the EGMS parents under OGH growth conditions, compared to Basmati 370, which had 1.1×10^{4} (highest). However, there was no significant difference in sterility or fertility among all the parental lines under either GH or OGH growth conditions.

Figure 8b shows the appearance of anther locules from EGMS grown outside the greenhouse. Under the light microscope, pollen grains were observed to fill the locules in B370 and in EGMS grown under greenhouse conditions (Figure 8a) and to stain blue-black with 1% KI (Figure 8c).

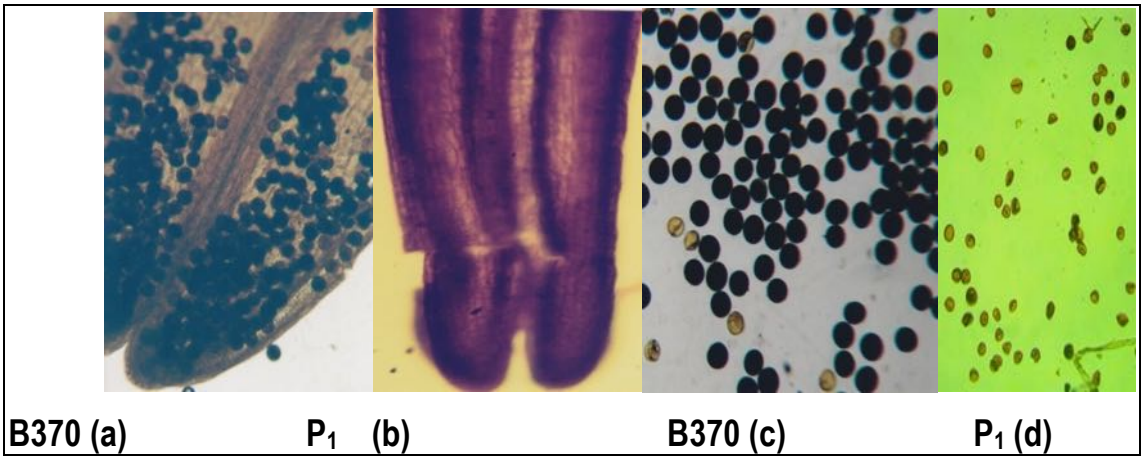

Figure 8: Comparison of pollen fertility (under x10 magnification) of plants grown in GH and OGH growth conditions. The anthers in (a) are from glumes in line B370 under GH growth conditions, while those in (b) were from EGMS (P_1) under GH growth conditions, respectively. Pollens shown in figures c and d were from B370 and P1, grown under GH conditions

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Blue-black pollen staining indicates pollen fertility [25]. Such pollen was observed mainly in Basmati (Figure 8a and c) under GH and OGH growth conditions, indicating that Basmati pollen was fertile at both high and normal temperatures and was not affected by photothermal-sensitive genic sterile genes. Figure 8c shows pollen stained blue-black, whereas Figure 8d shows pollen that appears dented and stained yellow with 1% KI, although all were grown under GH conditions, indicating that the pollen of P1 was more sensitive to temperature than that of BS370. Male sterility in P/TGMS rice is influenced by genes including *tms1, tms2, tms3, tms5, tms6,* and *tms9-1* [9]. Plants carrying these genes can be induced to become completely sterile under high-temperature growth conditions and then pollinated with donor pollen to produce hybrid seeds [12].

a (TGMS) **b (TGMS)** **c (TGMS)** **d (TGMS)**

Figure 9: Comparison of pollen and seed set rate (spikelet fertility) in GH and OGH conditions (under X10 magnification). Figures a and c show pollen grains from GH and OGH, respectively. However, b and d display spikelets from plants grown under GH and OGH conditions, respectively

Evaluation of hybrid lines

Basmati and EGMS (P1, P2 and T1) produced seeds after cross-pollination (Table 3), indicating potential for hybrid seed production. Hybrids from crosses between P1 x basmati217, P1 x basmati370, T x basmati217, T x basmati370, P2 x basmati217, and P2 x basmati370 were coded as P1B217, P1B370, TB217, TB370, P2B217, and P2B370, respectively. The hybrids were sown under greenhouse conditions and assessed for nine traits, including the number of productive tillers per hill, plant height (cm), days to 50% flowering, heading and maturity, panicle length and exertion (cm), percentage seed set, and 1000-grain yield per plant (grams). The mean performance of parents and hybrids—for traits such as height (HT), maturity day (MD), 1000 seed weight (1000SW), panicle exertion (PE), total glumes (TS), and filled spikelets

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(FS)—is shown in Tables 4 and 5. Plant height, detailed in Table 4, revealed that lines T (TGMS) measured 87 ± 0.7 cm, P1 (PGMS) measured 71.9 ± 0.6 cm, and P2 measured 77.8 ± 0.6 cm. Basmati 217 and B370 were the tallest plants, with heights of 145.6 ± 2.6 cm and 140.2 ± 2.1 cm, respectively. Hybrid heights ranged from 106.5 ± 1.3 cm to 119.3 ± 1.5 cm, with P2 x B370 being the tallest and T x B370 the shortest (Table 4). The EGMS lines had the fewest productive tillers (PT), whereas B370 had the most, with 29.6 ± 1.3. The F1 hybrids averaged between 24.2 ± 0.6 and 26.3 ± 0.8 productive tillers (Figures 7 and Table 4). Among the hybrids, P1 x B370 recorded 26.3 ± 0.8 PTs. Conversely, lines PGMS (P1 and P2) had the longest days to heading (HD), anthesis (AD), and maturity, followed by T (TGMS) and Basmati, which had the shortest (Table 4). The 1000-g seed weight for hybrid lines P1 x B217, P1 x B370, P2 x B370, and P2 x B217 ranged between 22.2 ± 0.1 and 23.1 ± 0.5, which was significantly higher than all parental lines (Table 4). However, TxB217 recorded the least weight of 19.2 ± 0.1 among hybrids. The 1000-grain weight of T, P2, and P2 lines was 17.5 ± 1.5, 19.1 ± 0.2, and 19.2 ± 0.1, respectively, while the pollen donors B217 and B370 measured 20.1 ± 0.3 and 20.1 ± 0.4, respectively (Table 4). Only T recorded a significantly lower weight than all other parents. The hybrid line TB370 had the longest panicle length (PL) of 26.5 ± 0.1, though not significantly different from B370, which measured 25.9 ± 0.2. Among the EGMS parental varieties, T had the longest PL (23.5 ± 0.2), which was significantly shorter than those of the other two EGMS lines (Table 5).

Lines P1, P2 and T had over 98% spikelet sterility, which was significantly lower than that of B217/B370 and F1 lines (Table 5). EGMS had significantly higher pollen sterility (114.3±1.8g) among the parental and hybrid lines. However, all hybrids had significantly higher PS than the parents (Table 5). All EGMS had significantly fewer filled spikelets than the parental and hybrid lines (Table 5). The F1S had the longest panicle exertions, ranging from 5.6±0.1d to 8.1±0.1f, followed by B217 and B370, with exertions of 4.8±0.1c and 3.8±0.1b, respectively. EGMS showed the lowest panicle exertion (Table 5). Hybrids P1B217, P2B217, and P1B370 exhibited higher TG but were not significantly different from B370 and B217.

Correlating parental and hybrid phenotypic traits

Correlations between heading date (HD), glume number (GN), fertile pollen (FP), and % sterility are shown in Table 6 for the parental varieties P1, P2, T, B217, and B370 grown under GH and natural environments. Fertile pollen showed r = 0.272 at $p < 0.01$ and $p < 0.05$, and % spikelet sterility was associated with sterile pollen (r = 0.145). A significant negative correlation was observed between HD and GN (r = -0.441). Other factors also showed clear relationships.

Phenotypic correlations among F1s, namely P1B217, P1B370, P2B370, P2B217, TB217, and TB370, are shown in Table 7. Seed weight was positively correlated

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only with PH and PT; all other correlations were negative (Table 7). Plant height (PH) showed significant positive correlations with productive tillers/panicles (r=0.286) and seed weight (r=0.336). Heading days were significantly positively correlated with FD and MD, with r=0.986 and r=0.967, respectively. Other negative correlations included PT and HD (r =- 0.109), PT and AD (r =- 0.117), PT and MD (r =- 0.109), SW and HD (r =- 0.126), SW and AD (r =- 0.167), and SW and MD (r =- 0.127).

Days to heading (HD), anthesis (AD), and maturity (MD) showed a strong positive correlation across all varieties studied, with r-values ranging from 0.967 to 0.986. Their positive values were much closer to 1 than those of the other parameters studied.

Unpaired t-test results for both GH and OGH growth environments showed a significant difference in days to heading at $p \leq 0.05$ (Table 5). The EGMS variety P1 had the highest p-value, followed by P2. Additionally, the t-test results in Figure 7 indicated that temperature level affects sterility, which in turn influences overall pollen viability. Under GH growth conditions, varieties P1, T, and P2 did not produce seeds, unlike those grown in the natural environment. Furthermore, lines B217 and B370 were partially sterile under GH growth conditions; they set fewer seeds than their counterparts under OGH growth conditions (Figures 7 and 9). There was a significant difference in days to heading and in pollen fertility percentage between EGMS grown under GH and OGH conditions.

Pollen sterility in lines P1, P2, and T grown under GH exceeded 97%, with very low seed set. This indicates a correlation between pollen sterility and seed set rate. Consequently, this correlation can be used to predict actual spikelet sterility in a hybrid rice breeding programme. TGMS and PGMS lines cultivated under high-temperature conditions have been reported to exhibit significantly reduced pollen fertility [30] at $p>0.05$. Lines P1 and P2 are PGMS, while T is a TGMS. PGMS sterility responds to long photoperiods. Although tropical regions typically experience about 12 hours of daylight, PGMS lines 1 and 2 had significantly lower fertility compared to Basmati 370 and 217. This also suggests that high temperature can effectively negate the long daylight requirement necessary to achieve 100% sterility in PGMS lines, which is essential to prevent adulteration of hybrid seeds with self-bred seeds during cross-breeding [20]. The results further suggest that sterility in the EGMS rice lines studied could be induced solely by high temperatures, without increasing daylight length.

Pollen sterility and spikelet sterility showed a weak positive correlation in EGMS grown under greenhouse conditions (Table 6), whereas [31] reports a strong positive correlation. The positive correlation can be explained by programmed cell death [28], a phenomenon in which, after reaching a critical sterility point, EGMS pollen exposed

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to high temperatures during the critical sterility phase leads to abortion. Temperatures above 33°C and also below 11°C cause pollen abortion in P/TGMS rice [28, 30].

All F1S had shorter days to anthesis (AD), days to heading (HD), and days to maturity (MD) than the female parents, P/TGMS. The three traits in F1S from crosses between P1 and B217, P1 and B370, P2 and B370, P2 and B217, T and B217, and T and B370 fell between the EGMS and B370 parental lines, indicating mid-parent heterosis. The AD, HD, and MD for P1B217, P1B370, and P2B370 F1 hybrids showed no significant differences from those of B217. Generally, hybrids from crosses between Basmati217 and TGMS recorded the earliest days to heading, anthesis, and maturity (Table 4). For example, the earliest days for AD, HD, and MD were 86±0.2a, 87.5±0.2a, and 116.1±0.2a for the TB217 lines, while for the TB370 lines they were 87.9±0.2a, 89.1±0.2a, and 117.9±0.2a. This indicates they expressed heterosis.

The greenhouse structure optimises internal parameters essential for photosynthesis, including solar radiation, air temperature, relative humidity, and carbon dioxide (CO2) concentration [32]. These factors enhance plant vigour and promote early maturity. This may explain why plants grown under greenhouse conditions head and flower earlier than those grown in natural environments. High temperatures induce reproductive growth in rice [29]. Greenhouse conditions may have stimulated expression of the Hd3a gene [32], thereby promoting growth. The Hd3a gene, located within a quantitative trait locus (QTL), influences rice flowering time by promoting flowering under short-day (SD) light conditions. For a successful cross-breeding programme, flowering of male and female parents must be synchronised [18]. Therefore, the B217/or B370 pollinators grown under OGH had to be synchronised with the EGMS grown under greenhouse conditions. The Basmati parents flower earlier than EGMS (P1 and P2) but around the same time as line T. To address this, sowing was staggered: EGMS (P1 and P2) were sown 10 days earlier, followed by all other EGMS and Basmati pollen donors, with a 10-day interval to ensure pollen availability for cross-pollination. This approach ensured that whenever EGMS was flowering, a flowering Basmati (pollinator) was also available.

Elongation of rice internodes is one of the most important traits in hybrid rice production, as it influences plant height and pollination and underpins grain yield [33]. Panicle length (PL) and panicle exsertion (PE) varied under greenhouse conditions, with hybrids outperforming parental cultivars (Table 5). In rice, panicle length and exsertion are driven by elongation of the uppermost internode, which is controlled by the internode elongation gene eui1 [33]. Complete panicle exsertion depends on the eui1 gene and is affected by temperature [33 - 36]. Studies by Bardhan et al. and Yang *et al*. [37, 35] suggest that different temperatures induce

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varying levels of expression of the male sterile gene in P(T)GMS lines. Lower temperatures lead to higher expression of the *eui* gene and improved panicle exsertion, thereby enhancing cross-breeding efficiency [33]. Among the hybrid lines, TB370, P2B370, and P2B217 showed no significant differences from B217 and B370 in PL. All hybrids exhibited significantly higher PE than all parents (Table 5). The observations indicate that different traits display various forms of heterosis [38].

The results also show that hybrids had higher seed set (39-56%) than the parents. Lines P2B217, P1B370, and P2B370 performed significantly better than the best parent (Table 4). The higher yield in hybrids relative to parents can be attributed to hybrid vigour [38]. Some degree of F1 sterility was observed in crosses between EGMS and Basmati lines, indicating further potential to increase yield by addressing this issue. This type of sterility has been observed in hybrid plants from the indica and japonica subspecies [38]. Certain indica and japonica hybrids show normal spikelet fertility, in which case one or both parents of these crosses must possess a dominant wide-compatibility gene (*S5n*) [39]. Sterility and non-sterility are thought to be controlled by three alleles: S-5i (in indica), S-5j (in japonica), and S-5n from WC rice [39,38].

Allelic interactions at loci *S7, S8, S9, S15,* and *S16,* located on chromosomes 4, 6, 7, 12, and 1, respectively, cause sterility independent of each other [40]. Genotypes *S-5n/S-5i* and *S-5n/S-5j* result in fertile female gametes, but the *S-5i/S-5j* genotype produces semi-sterile panicles due to the partial abortion of female gametes, which is postulated to have occurred in this study, as evidenced by the overall percentage seed set rate being lower than expected.

Lines B217 and B370 were taller than all the EGMS (maternal parents) and the hybrids. Notably, the hybrids displayed heights intermediate between those of the Basmatis and the EGMS parents. These results align with the findings of Tua *et al*. and Kanya *et al*. [41, 42], who reported that hybrid rice has intermediate heights relative to its parents. However, this is influenced by cultivar type, the agro-ecosystems involved, and the agronomic practices applied [43]. Therefore, the production of hybrids with intermediate heights in the current study is significant because they can be used to breed plants shorter than Basmati rice, thereby reducing lodging.

Hybrid seeds weighed more than those from parental lines, such as EGMS and Basmati cultivars. Among the hybrid cultivars, all except TB217 had higher grain weights than both parents. An increase in grain weight also enhances rice yield. Heavier seeds are preferred because they are healthier, contain more nutrients, and produce heavier seedlings with more roots when planted. Conversely, small seeds are associated with reduced seedling vigour and are difficult to harvest mechanically.

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Grain length (GL), thickness, and width determine grain size and cooking quality. These three traits—grain length (GL), thickness, and width—are quantitatively inherited and controlled by several genes [44]. So far, five key genes regulating seed size in rice have been identified: *GS3, GW2, qSW5 or GW5, GIF1*, and *GS5* [45, 44]. The gene *GS3* mainly influences seed length, while qSW5/GW5 and GW2 affect both grain width (GW) and weight in rice. According to Yoshida, Sirajul et al. and Zhang *et al.* [49 - 51], 1000-grain weight is a stable genetic trait in rice.

All control varieties grown in OGH at an average temperature of 23°c-24 °c had viable pollen ranging from 63% to 73% (Figure 8). These conditions are suitable for EGMS seed multiplication. Therefore, the Mwea site is appropriate for EGMS seed multiplication, while the GH environment can be utilised to induce sterility in EGMS varieties for hybrid seed production.

Hybrid rice seed production has been practised in countries such as China and India (24). Hybrid rice seed production technology has improved food security in China, resulting in a limited increase in rice prices that has benefited poor consumers. The technology has spread to many countries, including India [13] and South Korea [46], among others.

CONCLUSION AND RECOMMENDATIONS FOR DEVELOPMENT

High daytime temperatures above 34°C and nighttime temperatures of 20°C were effective in emasculating both PGMS and TGMS varieties in Mwea, Kenya (with 12 hours of daylight and 12 hours of darkness). This indicates that high temperatures during a 12-hour daytime length compensate for the over 13 hours of daytime needed to induce complete male-gamete sterility in PGMS, while use of a greenhouse to moderate diurnal temperature fluctuations increases male-gamete sterility in TGMS. This achievement enables the production of hybrid seeds in Kenya and in tropical countries using the EGMS method. Significant improvements in major yield traits, such as particle size and grain weight, among hybrid lines are a major progress in Basmati rice yield improvement. Overall, basmati370 showed greater heterosis than Basmati 217 across most traits.

Similar experiments to be conducted on a large scale outside the greenhouse in areas that attain temperatures above 34 degrees during the day and 22 degrees at night, such as the coastal and North Eastern regions of Kenya. This will take hybrid seed production out of the greenhouse, enabling upscaling. Also, with an over-25 % yield advantage, it will be viable to use a large-scale greenhouse for hybrid basmati seed production. Significant heterosis in PH, TT, HD, FD, and MD can be used to improve basmati rice yield. Considering some challenges in using P/TGMS, hybrid vigour can be fixed using doubled haploid technology, enabling the use of seeds in

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subsequent generations without loss of vigour and at a reduced cost compared with conventional hybrid seed production.

The Ministry of Education and Agriculture needs to allocate more funds for large-scale hybrid basmati rice production to improve yields to meet consumer demand. Also, research should be expanded to use molecular-assisted selection (MAS) in breeding and production of hybrid seeds.

Breeders need to work with the Kenya Plant Health Inspectorate Services to enhance local hybrid rice seed production instead of relying on imported seeds.

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Table 1: **Schematic representation of pollen fertility/sterility graduation [21]**

% sterile pollen	Category	% fertile pollen
0–20	Fully fertile (FT)	81–100
21–40	Fertile (F)	61–80
41–70	Partially fertile (PF)	31–60
71–90	Partially sterile (PS)	11–30
91–99	Sterile (S)	1–20
100	Completely sterile (CS)	0

Table 2: **Unpaired *T*-test analysis of % viable/fertile pollen and sterility. Table 2a shows pollen sterility under greenhouse environment (GH), while Table 2b shows pollen fertility under outside greenhouse (OGH) or natural growth conditions**

Table 2a

Varieties	GH growth conditions	*T*-test values	*p*-value (0.05)
P1	Percentage pollen sterility	$2.4*10^{-11}$	0.0001
T	Percentage pollen sterility	$1.6*10^{-10}$	0.0001
P2	Percentage pollen sterility	$3.3*10^{-11}$	0.0001
B217	Percentage pollen sterility	$5.6*10^{-12}$	0.0001
B370	Percentage pollen sterility	$3.9*10^{-12}$	0.0001

Table 2b

Varieties	OGH growth conditions	*T*-test values	*p*-value (0.05)
P1	Percentage pollen fertility	$6.9*10^{-11}$	0.0001
T	Percentage pollen fertility	$5.7*10^{-8}$	0.0001
P2	Percentage pollen fertility	$1.3*10^{-8}$	0.0001
B217	Percentage pollen fertility	$2.5*10^{-5}$	0.0001
B370	Percentage pollen fertility	$1.1*10^{-4}$	0.0001

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Table 3: Total number of F_1 seeds produced. Males and females were crossed to get F_1 seeds. Without B217/B370 pollination (cK) means that female parents were left to grow with no deliberate transfer of pollen

Female parent / Male parent	P1 (V1) %	P2 (V2) %	T1(V3) %
B217	7.20	11.47	39.12
B370	18.05	20.41	9.01
Without B217 pollination	0	0	0
Without B370 pollination	0	0	0

Table 4: Hybrids and Parental varieties' morphological traits

VAR	N	HT(cm)	PT(number)	HD (days)	DA(days)	DM (days)	1000 grain SW (g)
P1	92	71.9±0.6^{a}	19.7±0.7^{ab}	110.2±0.7^{b}	112.7±1.3^{e}	140.1±0.7^{d}	19.1±0.2^{b}
T	94	87 ±0.7^{b}	18.4±0.8^{a}	99.1±0.3^{bc}	101.7±0.3^{bcd}	129.3±0.3^{bc}	17.5±1.5^{a}
P2	90	77.8±0.6^{a}	22.7±0.6^{bc}	114±0.6^{e}	116.8±0.6^{f}	144.2±0.6^{e}	19.2±0.1^{b}
B217	91	145.6±2.6^{f}	25.4±0.9^{c}	99.5±0.5^{bc}	102.4±0.5^{cd}	129.8±0.5^{bc}	20.1±0.3^{bc}
B370	92	140.2±2.1^{f}	29.6±1.3^{d}	100.8±0.4^{c}	103.2±0.5^{d}	130.8±0.4^{c}	20.1±0.4^{bc}
P1B217	90	115.2±1.6^{de}	25.5±0.7^{c}	100±0.4^{bc}	101.5±0.4^{bcd}	130.2±0.4^{bc}	22.2±0.1^{de}
TB217	92	107.8±1.1^{c}	24.2±0.6^{c}	86±0.2^{a}	87.5±0.2^{a}	116.1±0.2^{a}	19.2±0.1^{b}
P2B217	93	116.9±1.6^{e}	25.6±0.7^{c}	98.2±0.3 ^{b}	99.7±0.3^{b}	128.2±0.3^{b}	22.2±0.4^{de}
P1B370	96	109.5±1.8^{cd}	26.3±0.8^{cd}	99.5±0.4^{bc}	100.8±0.4^{bcd}	129.7±0.4^{bc}	23.1±0.5^{e}
TB370	95	106.5±1.3^{c}	24.8±1 ^{c}	87.9±0.2^{a}	89.1±0.2^{a}	117.9±0.2^{a}	21±0.3^{cd}
P2B370	92	119.3±1.5^{e}	24.4±0.7^{c}	99±0.6^{bc}	100.4±0.5^{bc}	128.6±0.6^{bc}	22.7±0.2^{e}

Values before the ± sign are means of variables per plant. Means with different superscript letters within a column are significantly different ($P < 0.05$). N = number of plants sampled per variety under GH growth conditions. SW = 1000 per variety, Variety =VAR, Height =HT, Productive tillers =PT, Heading day=HD, Days to Anthesis =DA, Days to Maturity = DM, 1000 seed weight =SW

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Table 5: Other morphological traits for hybrids and parental varieties under GH conditions

VAR	N	PL(cm)	PE(cm)	TG	FS (grains)	PS	%SS
P1	276	18.8±0.2^{a}	0.1±0^{a}	90±1.8^{a}	0.7±0.3^{a}	89.2±1.8^{ef}	99.3±0.3^{d}
T	282	23.5±0.2^{b}	0±0^{a}	116±1.9^{cd}	1.7±0.4^{a}	114.3±1.8^{g}	98.9±0.3^{d}
P2	270	19.2±0.1^{a}	0±0^{a}	96.3±1.5^{a}	0±0^{a}	96.3±1.6^{f}	100±0^{d}
B217	273	25.3±0.2^{c}	4.8±0.1^{c}	122.9±2^{cde}	37.1±1.4^{b}	85.8±2^{e}	69.5±1.1^{c}
B370	282	25.9±0.2^{cd}	3.8±0.1^{b}	126.9±1.7^{e}	34.3±1.3^{b}	92.7±1.9^{ef}	72.6±1.1^{c}
P1B217	270	25.3±0.1^{c}	5.9±0.1^{d}	128.2±1.5^{e}	68.5±1.2^{e}	59.7±1.2^{abc}	46.4±0.7^{a}
TB217	273	25.6±0.1^{c}	8.1±0.1^{f}	115.9±1.4^{c}	49.4±1^{d}	66.5±1.4^{cd}	57±0.8^{b}
P2B217	279	24.1±0.2^{b}	5.7±0.1^{d}	124.6±1.9^{de}	69.5±1.4^{e}	54.6±1.1^{a}	44.4±0.7^{a}
P1B370	279	25.2±0.2^{c}	6.8±0.3^{e}	126.4±2.1^{e}	53.6±2^{d}	72.8±1.8^{d}	58.8±1.1^{b}
TB370	285	26.5±0.1^{d}	6.7±0.1^{e}	85.8±1.7^{b}	42.9±1^{c}	63.6±1.4^{bc}	59.6±0.7^{b}
P2B370	282	24±0.1^{b}	5.6±0.1^{d}	114.3±2.1^{c}	67±1.7^{e}	58.9±1.1^{ab}	47.5±0.7^{a}

Values before the ± sign are means per plant. Means with different superscript letters within a column are significantly different (P < 0.05). SD = standard deviation of the mean. Varieties (VAR), Panicle length (PL), Panicle exertion (PE), Total glumes (TG), Filled spikelets (FS), Pollen sterility (PS), Percentage spikelet sterility (%SS)

Table 6: Pearson correlation coefficients of heading date (HD), glume number (GN), Sterile pollen (FP) and % spikelet sterility (SS) of parental varieties

	HD	GN	FP	%SS
HD	1	-.441**	.272**	-0.054
GN		1	0.056	-0.017
SP			1	.145*
%SS				1

**Values with two asterisks indicate that the correlation is significant at P<0.0

*Values with one-star asterisks are significant at P < 0.05

A moderate negative correlation between HD and GN (r = -0.441, p < 0.01) was observed, while the correlation between HD and SP (r = 0.272, p < 0.01) and between SP and %SS (r = 0.145, p < 0.05) displayed a weak positive correlation. Relationships between GN and SP, GN and %SS, or HD and %SS were not significant

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Table 7: **Pearson correlation coefficients for plant height (PH), productive tillers (PT), heading day (HD), anthesis day (AD), maturity day (MD), and 1000 seed weight per plant (SW).** Values in parentheses indicate the correlation is significant at P<0.01**

	PH	PT	HD	AD	MD	SW
PH	1	.286**	-.296**	-.295**	-.298**	.336**
PT		1	-.109**	-.117**	-.109**	.195**
HD			1	.986**	.980**	-.126**
AD				1	.967**	-.167**
MD					1	-.125**
SW						1

The correlation between PH and SW ($r = 0.336$, $p < 0.01$) was notably positive, while the correlations between PH and HD ($r = -0.296$, $p < 0.01$), AD ($r = -0.295$, $p < 0.01$), and MD ($r = -0.298$, $p < 0.01$) were significantly negative. A weakly significant correlation was observed between PT and other variables. Correlations ($r > 0.96$, $p < 0.01$) indicate that HD, AD, and MD are highly interrelated, suggesting a high risk of multicollinearity. The correlation between SW and HD, AD, and MD was weakly negative; however, it was positive with PH and PT

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