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RESEARCH ARTICLE

Elevated Temperature Disrupts Pollen-Pistil Dynamics and Seed Set in Okra (*Abelmoschus esculentus* L. Moench)

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Elevated temperature can interfere with pollen formation and function in okra (*Abelmoschus esculentus*). The study was aim to quantify the impact of elevated temperatures on the reproductive stage in okra. In both the stain analysis and pollen tube growth test, pollen viability was decreased at elevated temperatures. The highest number of non-viable pollen grains were observed at 35°C and 40°C. The stigma was nonsignificantly high in receptivity at all temperatures; however, the seed set showed a significant decline under elevated temperatures. The findings offer the potential to look further into approaches, to genetic enhancement of heat-tolerant plants that will secure *okra* productivity during future climatic variation.

Key Words: Fertility, Fruit formation, Heat stress, Pollen, Stigma receptivity

Introduction

The rise in temperature due to global warming is a concern in many parts of the world (Anderson *et al.*, 2017; Feng *et al.*, 2017; Lobell and Asseng 2017). A report said, a 2°C increase would greatly exacerbate extreme weather, rising sea levels, loss of ecosystems, arctic melting, and other impacts (Anonymous, 2018). Even if governments were to implement their pledges fully, the world would face a rise in mean temperatures of 2.4 to 3.8°C by 2100. Elevated temperature caused an adverse impact during specific development of pre-zygotic and post-zygotic stages in okra (*Abelmoschus esculentus* L. Moench) (Ganpat and Isaac, 2015; Müller *et al*., 2016 and Broussard *et al*., 2017). Sexual reproduction of okra is sensitive to elevated temperature with reproductive tolerance up to 30 to 32°C (Arulrajah and Ormrod, 1973; Mangrich and Saltveit, 2000; Rahman *et al.*, 2012). Increased temperature caused adverse effects on seed set, which results in reduced seed dormancy and final seed yield due to alteration in floral development (Hoque *et al.*, 2016; Balasubramanian *et al.*, 2006; Oloumi and Rezanejhad, 2009). Responses may differ significantly between ecotypes of the same species (Madan *et al.*, 2012; Huang *et al.*, 2014). While temperature sensitivity has been extensively studied using leaves and roots (Iba, 2002; Yamaguchi-Shinozaki and Shinozaki 2006, Kotak *et al*., 2007; Wahid *et al*., 2007; Aubry-Kientz *et al*., 2019). Studies on sexual reproduction are more complicated because gamete development and fertilization are complex processes occurring during a short period, and predominantly hidden within the flower. Pollen-pistil dynamics under elevated temperature in okra requires elucidation. The study was undertaken to determine the influences of elevated temperature on pollen-pistil dynamics and seed formation in okra.

Material and Methods

Okra seed, cv. Clemson Spineless (CS), was obtained from the National Agriculture Research and Extension Institute (NAREI), Guyana, South America. On the Sixteenth day of September seeds pretreated with pesticides were sown into the potting mix soil in the germination tray. Water was provided immediately after sowing and then every day in the morning and afternoon until plants were 21 days old. While seedlings were developing seedbeds under the shade house were measured and arranged in a completely randomized design (CRD) with 3 replications of 4 treatments on 12 plots, the beds are denoted as plots. Soil preparation of the plots included the incorporation of poultry manure where 25 kg of manure per plot were added and mixed with the soil, then allowed to rest for 5 to 7 days before planting. All recommended agronomic practices were

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followed to raise the right crop. Soon the plots were ready for planting.

Developed seedlings in the germination tray were transplanted onto the prepared CRD plots inside the shade house on the sixth day of October. In each plot, seedlings were planted in double rows with 6 plants in a row, 12 plants per plot, with a spacing of 88 cm within the row and 90 cm between rows (Olczyk *et al*., 2005, 2006). Plots were $5m^2$ (5.0×1.0 m). Plants were watered immediately after transplanting and then continuously watered every morning and afternoon until plants matured and research was completed.

Pollen viability was determined with the Carmine Acetic Acid (CAA) stain using mature anthers (Sheidai and Fadaei, 2005). Carmine acetic acid stain was prepared by boiling a 40% acetic acid solution saturated with carmine. Flowers were harvested during morning hours and incubated for 2 h at 25 (control), 30, 35, or 40°C. Pollen grains were dusted onto a slide containing 1-2 drops of CAA stain, allowing immersion of pollen in the stain for 20-30 min. Viability was determined by counting darker stained pollen (viable), non-stained, or lightly stained and ruptured pollen (non-viable), using an OPTIKA Compound Light microscope (Ponteranica, Italy) at 400× magnification.

Each morning, freshly opened flowers and buds one day after anthesis were harvested and incubated at each temperature treatment for 2 h. Placing un-dehisced anthers in incubators allowed anthers to dehisce exposing pollen grains. Temperature treated pollen was cultured onto basic pollen germinating medium (PGM) for 1 h. A slightly modified *in-vitro* pollen growth medium (Li *et al*., 1999) was prepared which contained 0.01% boric acid; 5 mM calcium chloride; 5 mM potassium chloride; and 1 mM magnesium sulfate. The pH 7.5 was maintained with 1M potassium hydroxide and 20% sucrose for the solid medium as a source of carbohydrate and 1.5% agarose for solidification of media. Pollen germination was observed with the OPTIKA Compound Light microscope. Pollen grains were considered to have germinated, or be viable when the pollen tube had gained a length equal to, or longer than, the diameter of the pollen grain. Bursting pollen grains were categorized by an irregular mass of cytoplasm and starch grains protruding from the cells (Adhikari and Campbell, 1998; Kakani *et al*., 2002).

Stigma receptivity was determined in 40 flowers from all replicates where flowers were emasculated 1 day before anthesis. Immediately after emasculation, the flowers were placed within paper bags to prevent unwanted pollination. Receptivity of stigma was studied the next day (day 2). Emasculated flowers were harvested during morning hours and placed in an incubator for 2 h at 25, 30, 35, or 40°C. After removal from the incubator; the stigma surface was cut with a sharp razor blade, and 6% hydrogen peroxide solution (H_2O_2) was applied on the cut (decapitated) surface with a dropper. The appearance of bubbles within 2 to 3 min on the stigma surface indicated it was receptive, according to the methodology proposed by Silva *et al.*, 2013 and Gupta *et al*., 2015.

Approximately 20 mature unopened flowers per replicate of all treatments were hand-emasculated a day before hand-pollination. Emasculated flowers were covered in paper envelopes to prevent unwanted pollination. The next morning between 8.00 and 10.30 am, open flowers and dehisced anthers were collected and brought to the laboratory; where the flowers with exposed pollen grains were treated at 25, 30, 35, and 40°C for 2 hours. On the same day, the flowers were artificially pollinated by dusting with temperature-treated pollen, collected from incubated flowers, directly onto the stigma surface of the emasculated flowers. Pollinated flowers were bagged, and set aside to determine if fertilization occurred. Pistils were left on plants until maturity to determine seed sets with continuous monitoring. On day 12 following pollination, mature fruit was collected, and the seed set was counted. Statistical analysis was conducted using Analysis of Variance (ANOVA) in Statistics 10.

Results and Discussion

Pollen viability and germination

To test whether high-temperature influences pollen viability in *A. esculentus*, temperature-treated pollens were stained with carmine acetic acid. Consequently, a higher number of lightly stained, unstained, and ruptured pollen was noted for higher temperature treated pollen. In contrast, the proportion of darkly stained pollen was noted higher in number at ambient temperature treatment of 25°C. Hence overall pollen viability was recorded, substantially lower for increased temperatures, with a mean percentage of 70.1% at 40°C with 74.98% at 35°C and 79.8% at 30°C, respectively (Fig. 1a). On the contrary, at an ambient temperature of 25°C mean percentage was 82.0%, respectively. This suggested

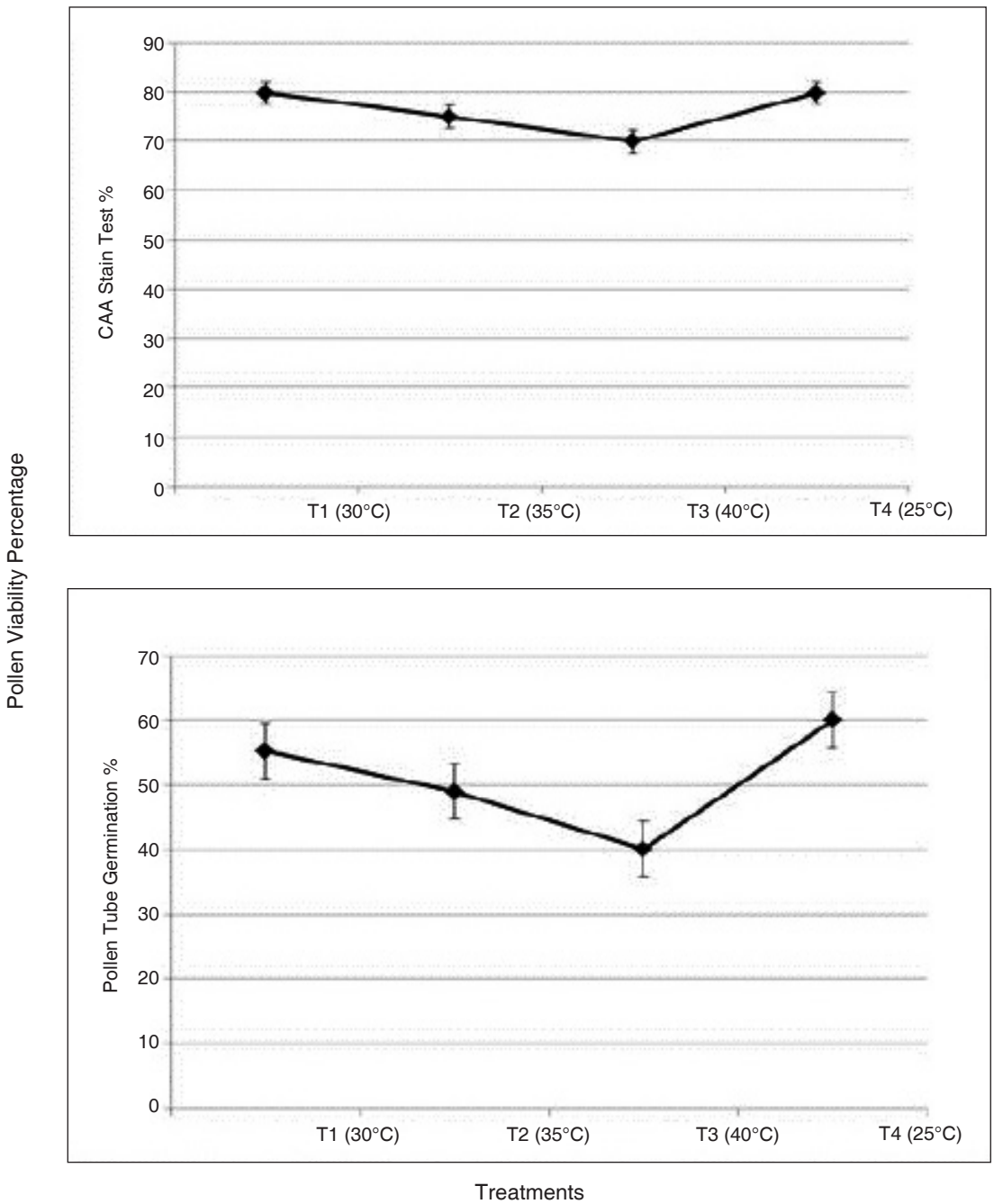

Fig. 1. Temperature effect on pollen viability: pollens in CAA stain (a) and pollen growth medium PGM (b)

that there was a significant effect of high temperature ($P < 0.05$) on pollen viability. The highest temperature (40°C) showed the least viable pollen grains, while the control (25°C) had the highest count of viable pollens. The highest pollen germination rates for the *A. esculentus* were detected (i.e. 60.02%) at an optimal temperature of 25°C (control). The germinability decreased to 55.28% at 30°C, 49.02% at 35 ºC, and 40.1% at 40°C (Fig.1b). Darkly stained pollen is regarded as highly viable, while the lightly stained or unstained, or ruptured were considered non-viable (Fig. 2a-c). Pollen germination percentage was calculated as the proportion of pollen grains germinated to the total number of pollen grains observed (Fig. 3 a-b). Analysis of variance (ANOVA)

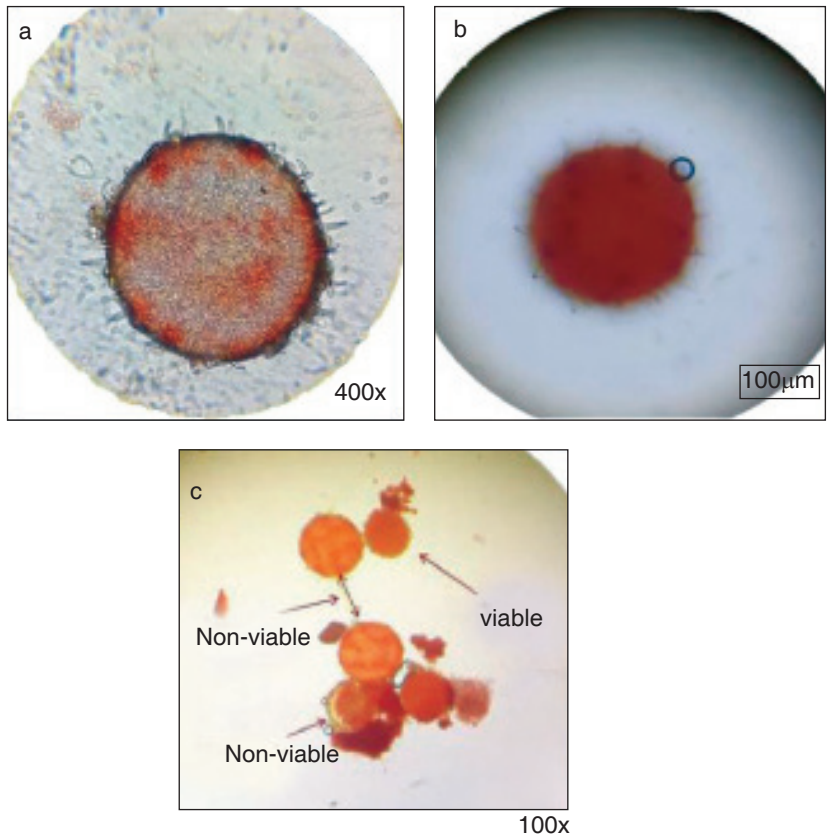

Fig. 2. Pollen viability of *A. esculentus* stained with CAA, non-viable (unstained) pollen (a), viable pollen (darkly stained) (b), and both viable and nonviable (C).

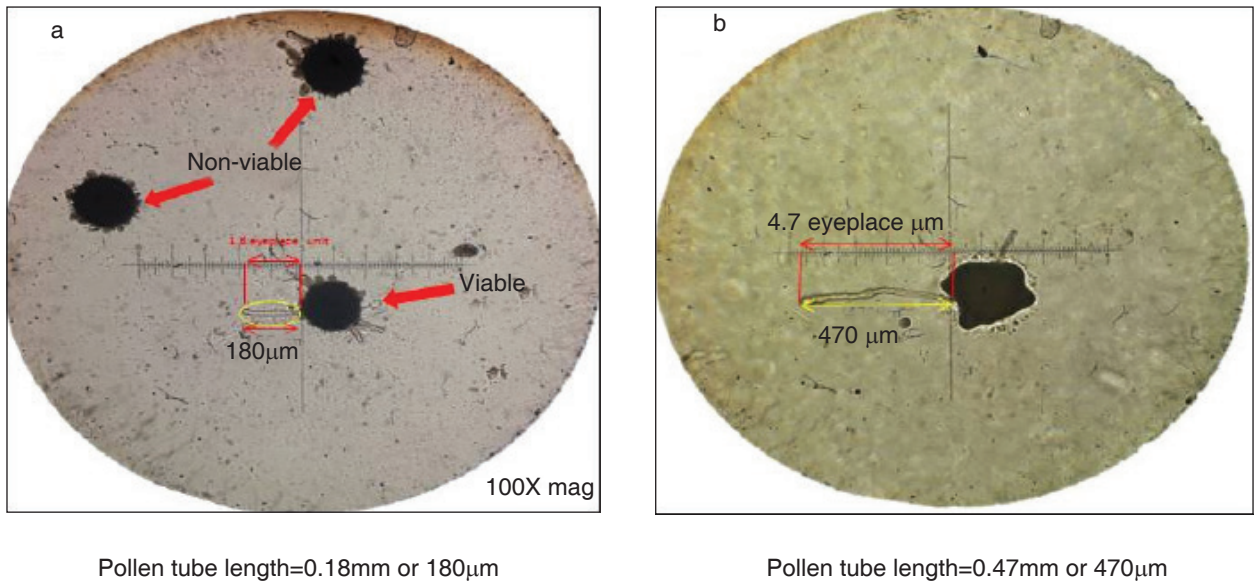

Fig. 3. *In-vitro* pollen tube elongation of viable and non-viable pollen of *A. esculentus* on pollen germination medium observed under the compound microscope (a) and (b)

showed that the higher temperatures had significant effects on pollen tube elongation, reducing pollen viability ($P < 0.05$). It is widely accepted that sexual reproduction in plants is highly vulnerable to temperature (Hedhly *et al.*, 2003; Hedhly *et al.*, 2009). The greatest sensitivity to an elevated temperature at early reproductive stages found in this study was declined pollen viability in stain test and *in-vitro* pollen germination of okra with reduced seed set. As many studies had shown pollen viability in the number of crops such as tomatoes (Müller *et al*., 2016), Arabidopsis (Huang *et al*., 2014), rice (Liu *et al*., 2004), and peach (Herrero and Arbeloa, 1989) is reduced at elevated temperatures. Earlier studies on cotton pollen have shown that temperatures (>30°C) inhibit *in-vitro* pollen growth and pollen tube penetration into pistil structures (Barrow, 1983; Kakani *et al.*, 2005).

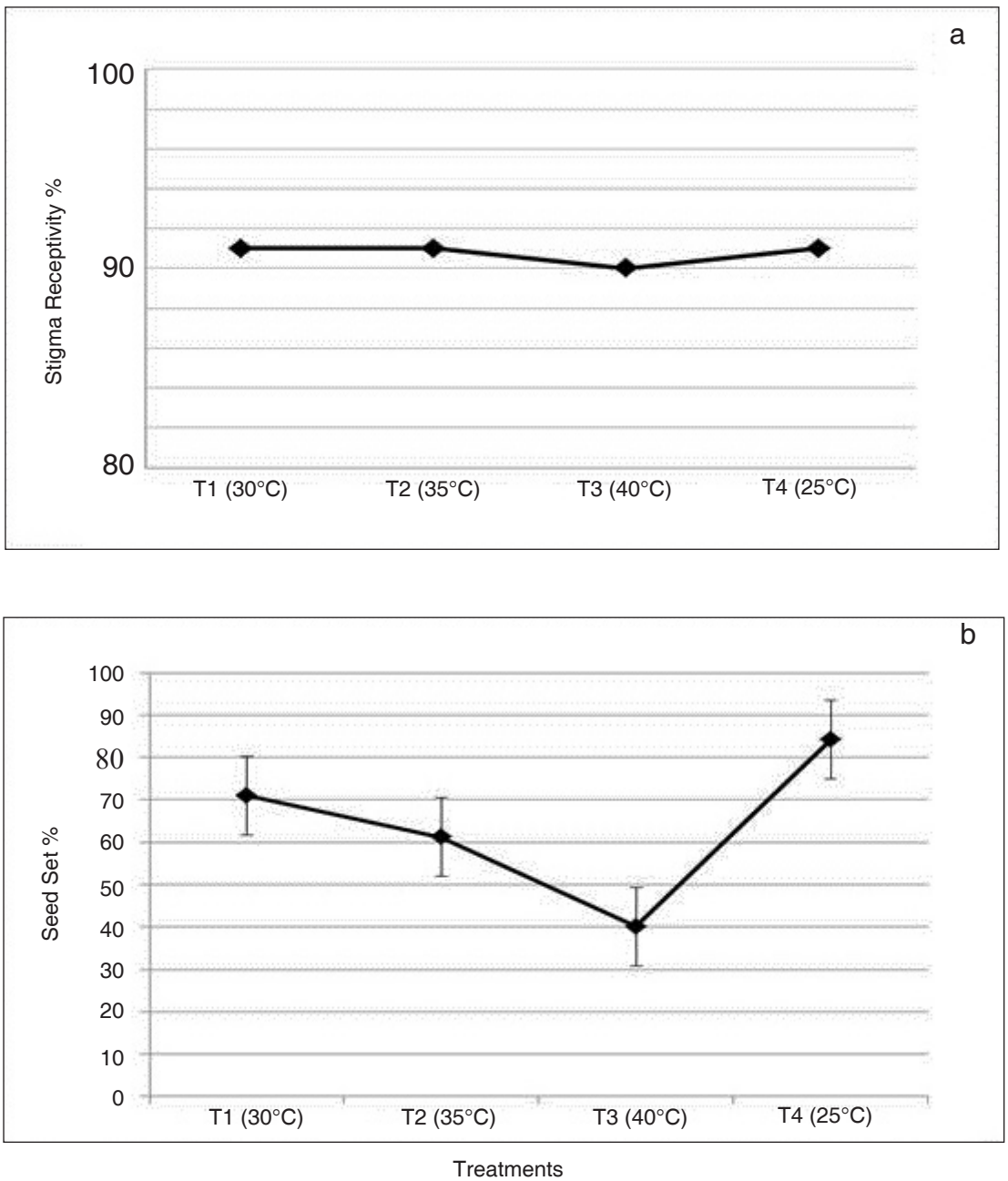

Fig. 4. Stigma receptivity (a) and seed set (b) under different temperature treatments. For (a) the p-value = 0.8018; with no significant difference in stigma receptivity with an increase in temperature. For (b) the p<0.05 with a significant difference in seed set with an increase in temperature.

In the current study, a significant percentage of pollen viability was observed amongst varied temperatures 35 to 40°C showed reduced viable pollens with deteriorated microspore cytoplasmic contents, which appeared as lightly stained or unstained. The percentage for non-viability in pollen was recorded, 70.1, 74.9, and 79.8% at high-temperature, 40, 35, and 30°C respectively, compared to control that showed viability percentages of 82.01% with darker stained pollens. *In-vitro* pollen germination n showed reduced pollen viability percentage, 55.21, 49.0, and 40.1% at temperatures 30, 35 to 40°C respectively. That contributes to a much lower proportion of pollen tube elongation; considerably tube length had not exceeded the substantial diameter of the pollen. On the contrary, it was found that dynamic tube elongation at 25°C of temperature having 60.02%. Therefore, the higher temperatures had a significantly negative impact on the feasibility of male gamete and consequently hindered the reproductive processes in plants reducing yield.

Stigma receptivity

The analysis of variance (ANOVA) showed that various temperatures of, 25, 30, 3,5 and 40°C respectively had no significant effect on stigma receptivity (P>0.05) (Fig. 4a). Generally, all-temperature treated samples had a similar trend, i.e., 91, 91, 91, and 90% for 25, 30, 35, and 40°C, respectively. In all the analyzed flowers, stigma was fully receptive. Oxygen bubble formation within 1-3 minutes observed on the stigmas was considered receptive (Fig. 5a). Elevated temperatures had no significant effect on stigma receptivity. All different temperatures *i.e.,* 25, 30, 35, and 40°C recorded a receptivity percentage of stigma ranging between 90–91%. For instance, pollen has been reported to be more sensitive to higher temperatures than female reproductive structures (Balasubramanian *et. al*., 2006). However, the effects of high temperature on female fertility could not be disregarded (Mangrich and Saltveit, 2000; Porch and Jahn, 2001). The previous report revealed that exposure to a high-temperature response in snap bean did not significantly affect stigma receptivity (Dickson and Boettger, 1984). Studies with Indian mustard (*B. juncea*) suggested vulnerability in stigma receptivity when exposed to high temperature during at flowering stage (Maity *et al*., 2019).

Seed Set

The temperature had a more significant effect on the seed-set; with the lowest seed set of 40.1% that was obtained under an elevated temperature of 40°C followed by a 5°C temperature treat with mean having 61.23% seed set (Fig. 4b). Seed-set was reduced by increased temperatures with a significant relationship between seed set and elevated temperature ($P < 0.05$) (Fig. 5b-c). It was evident that the highest seed set (84.21 %) was found under ambient temperature (25°C) treatment followed by treatments under 30°C of temperature (70.9%). Likewise, higher temperatures also instigated bell shape fruit formation (Fig. 5d). The result indicated that the elevated temperature decreased seed set count and allowed the deformation of fruits. There was an obvious negative relationship obtained between temperature and seed set. The effects of temperature above the critical temperatures (35/40°C) had recorded a reduced seed set supported by the previous studies showed a reduction in pollen viability and seed set in beans (Monterroso and Wien, 1990; Gross and Kigel, 1994). In our study, there was no effect on the fertilization process and seed set at 25°C; however, the seed set number decreased as temperature increased above 30, 35 to 40°C. Interestingly, fruits produced at temperatures 35 and 40°C were noticed to have taken bell-shaped and did not have fully developed seeds. Thus, it is determined that after exposure to temperatures 30, 35, and 40°C, respectively, there were fewer pollen grains per flower that remained viable. Consequently, studies suggested that reduced seed-set at higher temperatures is likely a result of lower anther dehiscence and pollen sterility (Monterroso and Wien, 1990; Gross and Kigel, 1994). Homogenous effects on pollen development and fruit-set have been observed in peanut (Prasad *et al*., 2002, 2003), cowpea (Hall, 2004), and tomato (Peet *et al*., 1998). Generally, plant response to high temperature was found to be most severe during periods of rapid growth and development (Hoque *et al*., 2016). Little tolerance of pollen development to heat stress has been reported in Chinese cabbage (Kuo *et al.*, 1981) and bottle gourd (Iapichino and Loy, 1987). Gibberellin regulates floral developments (Gupta and Chakrabarty, 2013) thus; an increase in temperature leads to GA-deficiency that caused flower mutation typically having short stamens as a result of reduced cell extension within the filaments the lowest pod set was observed in snap bean when flower buds were exposed to heat, which gradually decreased floral development affecting young pods and seed-set rate (Dickson and Boettger, 1984).

The elevated temperature adversely affects the male reproductive phase in *A. esculentus*, which is amongst

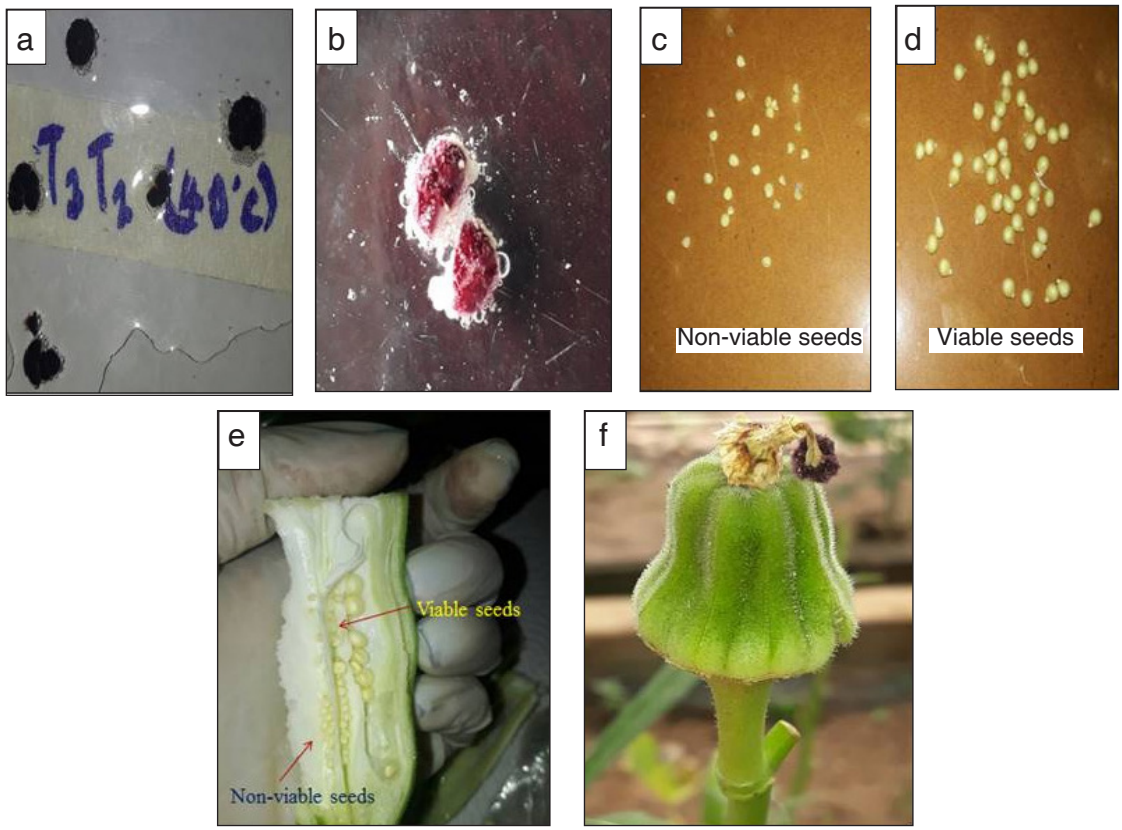

Fig. 5. Female reproductive structure (stigma) of *A. esculentus* with numerous oxygen bubbles on the stigma after reaction with hydrogen peroxide (a-b). Seeds not fully developed; reduced in size and irregular shaped (Non-viable seeds) (c), seeds fully developed; larger in size and plump shaped (Viable seeds) (d), viable and non-viable seeds attached to Okra fruit, obtained after artificial pollination from higher temperature exposed pollen (e). A view of Okra fruits that formed bell-shaped structures (deformed fruits) at elevated temperature treatments; hence seed set and quality of yield hindered (f).

the most susceptible process displaying negative impacts on plant fertility, leading to declined seed set and deformity in fruit formation at (>35°C) exhibiting reduced male fertility. In contrast, stigma receptivity indicated consistency tolerance to merely all temperatures. This study also reports a better understanding of the okra plant's capability to cope with heat stress during reproductive development. To identify potential genetic traits, thus implementing strategies to improve plant heat stress tolerance. This study also delineates the benefits to forestry and agricultural practices shortly as increasing temperatures pose threats to production yield.

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Declaration of interest statement

Authors have no conflict of interest

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