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The Influence of Plant Growth Modulators on Physiological Yield and Quality Traits of Sesame (*Sesamum indicum*) Cultivars Under Rainfed Conditions

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Abstract Sesame is an important oilseed crop, and the crop yields frequently fluctuate as the crop is largely grown in rainfed and low-fertile lands. Limited water availability negatively affects many physiological processes and the final productivity of sesame. Limited work has been carried out in the past to understand the role of plant growth regulators (PGRs) in modulating sesame growth and development for optimum productivity. A field study was conducted under rainfed conditions to evaluate the response of foliar application of different PGRs such as hormonal-based gibberellic acid (20 ppm); chemical-based thiourea (500 ppm); chemical-constituting structural component-based ortho-silicic acid (380 ppm); and control (water-sprayed) on sesame cultivars: Swetha til, GT-10, TKG-22, and JCSDT-26. The PGRs foliar application was done at the vegetative (25–30 days after sowing), 50% flowering (40–45 days after sowing), and seed development (70–75 days after sowing) stages of the crop. The results revealed that application of different PGRs positively influenced the plant's growth, physiological, yield and quality traits; however, most effective results were obtained with gibberellic acid (20 ppm), followed by ortho-silicic acid (380 ppm), and thiourea (500 ppm) improved the morphological, yield, and yield-attributing traits. The interaction between PGRs and varieties was found significant and among the sesame cultivars, swetha til followed by JCSDT-29 was found most promising. The application of PGRs has significantly improved the plant height, leaf area, number of branches, capsules, seeds/capsules, seed yield oil content, and fatty acid content compared to the control by gibberellic acid, followed by ortho-silicic acid and thiourea. The interaction between PGRs and varieties was found to be significant, and cultivar Swetha til, a white-colored cultivar performed most superiorly among the different tested cultivars in terms of growth, physiology, yield as well and quality traits when treated with GA₃ at 20 ppm. The seed yield was enhanced by 25–26%, 11–12%, and 6–7% with the application of gibberellic acid, ortho-silicic acid, and thiourea, respectively, over control. Considering the findings, it can be concluded that the application of PGRs (thiourea, ortho-silicic acid, and gibberellic acid) significantly enhanced the growth, physiology, yield, and quality of sesame under rainfed conditions; however, GA₃ at 20 ppm was found most effective and may not only enhance the optimum productivity but also effective in improving the quality traits of sesame.

Keywords Sesame · Plant growth regulators · Gibberellic acid · Ortho-silicic acid · Thiourea

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Abbreviations

PGRs	Plant growth regulators
GA ₃	Gibberellic acid
TU	Thiourea
OSA	Ortho-silicic acid
C	Control
DAS	Days after sowing
DFF	Days to first flower
DOF	Days to 50% flowering
DM	Days to maturity (DM)
PH	Plant height
NBP	Number of branches/plant
LA	Total leaf area
RWC	Relative water content
Pn	Photosynthetic rate
E	Transpiration rate
gs	Stomatal conductance
iWUE	Intrinsic Water Use Efficiency
CT	Canopy temperature
SCMR	SPAD chlorophyll meter readings
NCP	Number of capsules per plant
CL	Capsule length
CW	Capsule dry weight
NSC	Number of seeds/capsule
TW	1000-Seed weight
SYP	Seed yield/plant
HI	Harvest index
OC	Oil content

Introduction

Climate change is a serious threat and a prime concern across the globe for farming due to the higher vulnerabilities of plant systems and the insufficient in-built mechanisms to overcome the detrimental effects of harsh environmental conditions [45]. While rainfall patterns have a significant influence on quantitative and qualitative traits of oilseed crops [23, 50, 51, 61, 62], temperature profiles of the season also have a significant effect on sesame performance [56, 58, 63]. Several chemicals have been reported to enhance plant-in-built mechanisms for sustainable crop yields, either as foliar spray or as soil application [76]. The oldest oilseed crop, sesame (*Sesamum indicum* L.), known for its excellent oil quality, is largely cultivated during the rainy season with poor management and frequently gets exposed to the vagaries of rainfall. The crop is mostly grown for its seeds, which contain the highest amount of oil (nearly 44–55%), protein content (around 25%), and is rich in antioxidants such as sesamin (0.4–1.1%), sesamol (0.3–0.6%), and are resistant to oxidation, which is due to the presence of its endogenous antioxidant lignans along with tocopherols [11, 68].

Plant growth regulators (PGRs), either chemical-based or hormonal-based, could modulate plant mechanisms to enhance tolerance to abiotic stresses and further stimulate growth and yields [69, 75]. The available kinds of literature highlighted the promotive role of different plant growth-promoting substances in enhancing yield in various oilseed crops, particularly under water-limited conditions [6, 44, 48, 77, 86]. Plant growth regulators are recognized as low-cost and eco- and farmer-friendly technologies for enhancing the production and stress tolerance of standing crops under field conditions. Positive regulatory effects of foliar application of PGRs (thiourea, ortho-silicic acid, and gibberellic acid) on the growth and yield attributes [9, 10, 25, 36, 79, 80] have been reported elsewhere.

The use of hormonal-based PGR, gibberellic acid (GA₃), is becoming popular due to its promising effects on sesame through increasing the number of flowers per plant, number of pods per plant, seeds per pod, and weight of seeds per plant in sesame [9, 25, 36, 79]. Similar responses have also been noticed in soybean [26] and other oilseed crops such as mustard and safflower [39, 70, 72]. Ortho-silicic acid (OSA) is the only available form of silica for plants, and a PGR with a chemical-based and constituting structural component is reported to maintain plant water relations under stress conditions and ensure improved plant tolerance [69]. Few commercially available OSA formulations are widely used to enhance crop yields in wheat [59]; rice [42, 43]; and sorghum [27] under drought conditions. Thiourea (TU), a chemical-based PGR with an amine group, serves as a source of nitrogen (36%) and sulfur (42%), which helps in plant metabolism [54] through the redox-mediated mechanism for growth modulation [83, 84]. Significant improvements in antioxidant defense systems, nitrogen metabolism, plant water relations, and photosynthesis were observed upon foliar application of TU [30, 82]. Further, reports suggest that thiourea improves chlorophyll content, test weight, and stress tolerance [2, 40, 52, 73]. However, the role of TU in modulating the morphological, physiological, and biochemical aspects, particularly in sesame has remained unexplored.

These shreds of evidence indicated that PGRs play a crucial role in plants' morphological, physiological, biochemical, and crop yield traits. Yield limitations due to the vagaries of monsoons continuously threaten sustainable agricultural development, particularly in crops like sesame that are captives in rainfed situations. Lack of information on PGRs on quantity and quality traits, particularly in sesame under rainfed conditions, persists. Therefore, to enhance sesame crop yields under rainfed situations and economic returns, different PGRs were used to study the response of selected sesame cultivars for (i) to estimate the possible role of different PGRs in enhancing the morpho-phenological traits (ii) to understand how PGRs modulate

the plant physiological processes in sesame, and (iii) to quantify the effectiveness of PGRs in improving the seed yield and seed qualitative traits.

Materials and Methods

Experimental Site

The experiment was conducted at the ICAR-IIOR Research farm, Narkhoda, Hyderabad during the year 2019 in the *khari* season. The site is situated at 17°15'16" N latitude and 78°18'30" E longitude at an altitude of 542 m above mean sea level. Weather data during the crop growth period were recorded and presented in Fig. 1.

Experimental Material

A total of four sesame (*Sesamum indicum* L.) cultivars, *i.e.*, Swetha til, GT-10, TKG-22, and JCSDT-26, were selected for the experiment (Supplementary Table 1). The foliar application of PGR viz., gibberellic acid at 20 ppm, orthosilicic acid at 380 ppm, and thiourea at 500 ppm along with control (water spray) used as a foliar application at vegetative (25–30 DAS), 50% flowering (40–45 DAS) and seed development (70–75 DAS) stages. The selected varieties were similar in their phenological (40–45 days to 50% flowering) and maturity (90–93 days) behaviors and adapted to semi-arid conditions.

Crop Management and PGR Application

The experiment was designed in a factorial randomized block design (FRBD) with five replications. The soil at the experimental site was sandy loam soil belonging to the chalka soil series of Alfisols order with a poor water holding capacity of 18%. The soil pH was 7.6; EC was 0.36 dSm⁻¹; organic carbon was 0.41%; and clay content was 17.45%, as recorded at the experimental site. The available soil N, P, and K were 235 kg ha⁻¹, 23 kg ha⁻¹, and 401 kg ha⁻¹, respectively, during the experimentation. Each experimental unit was 12 m² in area, and the seeds were dibbled at a spacing of 45 cm (between rows) × 15 cm (between plants) during the first week of July 2019. The recommended fertilizer dose (40 kg N + 20 kg P₂O₅ + 20 kg K₂O/ha) was applied just before sowing. The PGRs were applied at vegetative (25–30 days after sowing), 50% flowering (40–45 days after sowing), and seed development (65–70 days after sowing) stages. The recommended standard package of practices was followed and

prophylactic measures against pests and diseases were followed to raise a healthy crop. The morphological and physiological observations were recorded at full flowering (50–55 days after sowing) and seed development (75–80 days after sowing) stages after 72 h of foliar applications of PGRs, whereas yield measurements were done at physiological maturity, at harvest and after harvest.

Physiological and Quality Traits Estimation

Phenological traits like days to first flower (DFF), days to 50% flowering (DOF), and days to maturity (DM): morpho-physiological traits such as plant height (PH), number of branches/plant (NBP), total leaf area (LA), relative water content (RWC); and photosynthesis-related traits such as photosynthetic rate (Pn), transpiration rate (E), stomatal conductance (gs), intrinsic Water Use Efficiency (iWUE), and canopy temperature (CT) were recorded at flowering (50–55 days after sowing) and seed development (75–80 days after sowing) stages after foliar applications of PGRs in 10 randomly selected plants in each treatment. The SCMR (SPAD chlorophyll meter readings) were also recorded at the above-mentioned intervals using SPAD-502 Plus (Konica Minolta, Inc.) The photosynthesis-related parameters were recorded using an infrared gas analyzer (LICOR 6400) from 10.00 to 13.30 h IST on fully sunny days. The upper 5th leaf from the terminal part of a three plants was selected for photosynthesis-related traits measurements. The relative water content (RWC) was recorded from the upper 3rd leaf from the terminal part of a plant (4–5 leaves and from 2 to 3 plants) taken after PGRs application and calculated using the formula $\{RWC = [(fresh\ weight - dry\ weight)/(turgid\ weight - dry\ weight)] \times 100\}$.

The yield and yield-attributing traits like number of capsules per plant (NCP), capsule length (CL), capsule dry weight/plant (CW), number of seeds/capsule (NSC), 1000-seed weight (TW), seed yield/plant (SYP), and harvest index (HI) were recorded in each replication from 10 randomly selected plants after harvest. Biochemical traits such as fatty acid profile and oil content were recorded from the seeds using gas chromatography, an Agilent 7860A, and a nuclear magnetic resonance spectrometer (NMARS), respectively.

Statistical Analysis

The aggregate mean values were subjected to statistical analysis. The essential statistics like variance and coefficient of variation were calculated using the method

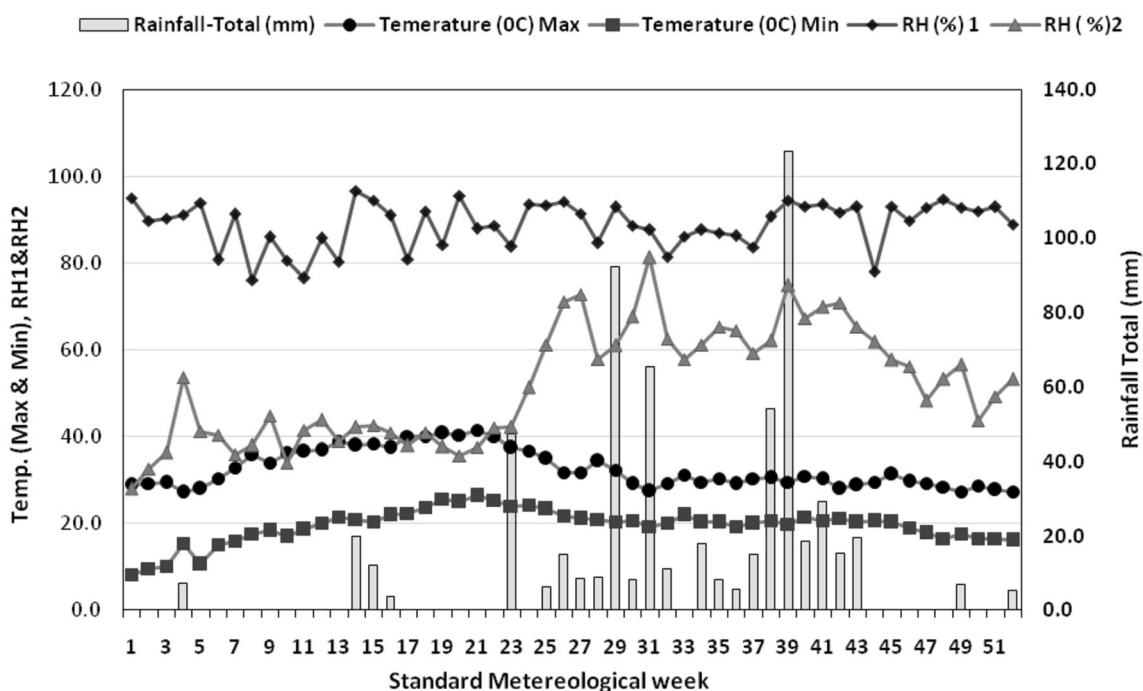


Fig. 1 Weekly meteorological data during crop growth recorded at experimental site (*Kharif* season 2019–2020)

described by Panse and Sukhatme [53]. The analysis of variance was analyzed using two factorial randomized block design to understand the significance of varieties, treatments and their interaction.

Results

Effect of PGRs on Different Morphological and Phenological Traits

The analyses of variance showed that significant differences among treatments (A), accessions (B), and replicates ($p < 0.05$) were observed for various recorded morphological traits. The results revealed that plant height ranged from 53.6 cm (GT-10) to 120.0 cm (swetha til) at the flowering stage. At the seed developmental stage, the range of variation was from 64.6 cm (GT-10) to 121.7 cm (swetha til). The maximum average plant height was recorded with the application of the mean of GA3 in all varieties at both flowering (87.8 cm) and seed developmental stage (112.7 cm); however, among the varieties, swetha til registered the highest plant height with the application of GA3 (20 ppm) at both flowering (120.0 cm) and seed development stage (121.8 cm). In addition, foliar treatment with OSA and TU also improved the plant height among all the sesame cultivars, and the highest plant height was observed in swetha til at both the flowering and seed developmental stages compared to the control

(Supplementary Table 2a). The leaf area varied from 482.0 (GT-10) to 1275.1 cm² (swetha til) and from 458.5 (TKG-22) to 1142.2 cm² (swetha til) at the flowering stage and seed developmental stage, respectively. Similar to PH, among the PGRs, the highest leaf area at both flowering (1147.4 cm²) and seed developmental stage (965.4 cm²) was recorded with the application of GA3, whereas among the cultivars, swetha til showed the highest leaf area compared to the rest of the cultivars. The trait total number of branches was recorded and found to vary from 4.80 (TKG-22) to 6.00 (swetha til), and the highest number of branches was noticed when plants treated with GA3 (5.60), followed by OSA (5.30), whereas treatment with TU (5.10) was found at par with the control. Among the cultivars, swetha til followed by JCSDT-29 and GT-10 had the highest number of branches.

The analysis of variance underpinned that there were significant differences among treatments (A), accessions (B), and replicates ($p < 0.05$). The crop phenology traits such as days to first flower varied from 39.0 (GT-10) to 47.3 days (TKG-22); days to 50% flowering from 53.0 (swetha til) to 56.3 days (TKG-22) and days to maturity from 86.3 (TKG-22) to 91.7 days (TKG-22). The mean performance indicated that the application of PGRs caused earliness in the phenology of sesame and a minimum number of days to first flower (39.9 days), 50% flowering (53.4 days), and days to maturity (87.1 days) were observed with the application of GA3 followed by OSA and TU. On the other hand, among the cultivars, swetha til

showed the earliest 50% flowering, while TKG-22 matured earliest (Supplementary Table 2b). Among the different PGR (GA, TU, and OSA), the application of GA₃ (20 ppm) was found promising and phenological traits such as days to first flower, days to 50% flowering and days to maturity showed earliness by almost 6–7%, 3–4%, and 3–4%, respectively.

Effect of PGRs on Different Physiological Traits

The per se performance revealed that PGRs had a profound effect on SPAD chlorophyll meter readings (SCMR). It was observed that the SPAD values ranged from 37.3 (TKG-22) to 51.5 (swetha til) at flowering and from 41.4 (TKG-22) to 61.7 (swetha til) at the seed development stage. Among the PGRs, the foliar application of TU, followed by GA₃ and OSA at both the flowering and seed development stages, was found to be most promising in improving the SPAD values compared to the control (Supplementary Table 3a and Fig. 2). The cultivar Swetha til recorded the highest SPAD values, followed by JCSDT-29, followed by the rest of the cultivars. The RWC varied from 70.6 (TKG-22) to 83.3% (swetha til) and 74.5 (TKG-22) to 85.9% (GT-10) at the flowering and seed development stages, respectively (Supplementary Table 3a and Fig. 3). The per se performance further showed that the application of TU at both flowering (82.9%) and seed developmental stage (85.5%) was most effective in maintaining a higher RWC, followed by GA₃ and OSA compared to control. On the other hand, among the cultivars, the highest RWC was reported in cultivar swetha til followed by GT-10 at both the flowering and seed development stages.

Maintaining a lower canopy temperature by plants is an adaptive mechanism under rainfed conditions. A lower canopy temperature (CT) favors optimum metabolic activities and plants achieve such conditions by increasing the water absorption and transpiring more water. The per se performance showed that rainfed conditions increase the plants' canopy temperature; however, application of PGRs significantly lowers the canopy temperature. The CT was varied from 29.3 (swetha til) to 31.3 °C (GT-10 and TKG-22) at the flowering stage, whereas from 29.0 (swetha til) to 30.7 °C (TKG-22) at the seed development stage. The minimum canopy temperature among the cultivars was recorded in swetha til followed by JCSDT-29. The lowest canopy temperature when treated with GA₃ at both flowering (30.1 °C) and seed development stage (29.4 °C), indicating that growth regulators have a direct role in maintaining favorable tissue water content and lowering the leaf temperatures (Supplementary Table 2b and Fig. 3). The application of OSA and TU also lowers the canopy

temperature at both the flowering and seed development stages compared to the control.

The results showed that the photosynthetic rate ranged from 9.8 (GT-10) to 18.9 $\mu\text{mol CO}_2\text{ m}^{-2}\text{ s}^{-1}$ (swetha til) and from 11.9 (GT-10) to 21.2 $\mu\text{mol CO}_2\text{ m}^{-2}\text{ s}^{-1}$ (swetha til) during flowering and seed development stage, respectively (Supplementary Table 3b). Likewise, transpiration rates showed a range of variation from 0.70 (GT-10) to 2.48 $\text{m mol H}_2\text{O m}^{-2}\text{ s}^{-1}$ (TKG-22) at the flowering stage, whereas 1.28 (JCSDT-29) to 2.25 $\text{m mol H}_2\text{O m}^{-2}\text{ s}^{-1}$ (TKG-22) at seed developmental stage. Data about stomatal conductance (gs) revealed a range of 0.66 (TKG-22) to 1.31 $\text{m mol H}_2\text{O m}^{-2}\text{ s}^{-1}$ (swetha til) and from 0.79 (GT-10 and TKG-22) to 1.36 $\text{m mol H}_2\text{O m}^{-2}\text{ s}^{-1}$ (GT-10) at the seed developmental stage (Supplementary Table 3c and Fig. 3). Substantial improvement was recorded concerning intrinsic water use efficiency (iWUE) under the influence of plant growth regulators (Supplementary Table 4a, Fig. 3). It was significantly varied at both flowering (9.1–19.2 $\mu\text{mol mol}^{-1}$) and seed development stage (10.3–24.8 $\mu\text{mol mol}^{-1}$). The mean data indicated that physiological traits such as photosynthetic rate, stomatal conductance, and intrinsic water use efficiency were found most promising with the application of GA₃ followed by OSA and TU, whereas treatment with TU and OSA was found most effective in lowering the transpiration rate among sesame cultivars. Among the cultivars, cultivar Swetha til followed by JCSDT-29 maintains a high photosynthetic rate, stomatal conductance, and intrinsic water use efficiency; however, the lowest transpiration rate was observed in TKG-22 followed by GT-10.

Effect of PGRs on Various Yield Contributing and Yield Traits

The various yield traits showed significant ($p < 0.05$) differences among the cultivars due to the application of different PGRs. The results showed that the yield-attributing traits such as capsule length {1.85 (GT-10) to 2.17 cm (swetha til)} capsule dry weight {4.5 (TKG-22) to 11.9 g (swetha til)}, number of capsule plant-1 {59.9 (TKG-22) to 108.8 (JCSDT-29)}, number of capsule plant-1 {58.0 (TKG-22) to 83.3 (swetha til)}, and test weight {2.30 (TKG-22) to 3.64 g (swetha til)} varied significantly (Table 1, Supplementary Table 4b, and Fig. 4). Among the different tested PGRs, the foliar application of GA₃ (20 ppm) followed by OSA (380 ppm) was found to be most effective in improving the yield-contributing traits of sesame cultivars compared to the control. Similarly, among the cultivars, swetha til, followed by JCSDT-10, was found to be superior compared to the rest of the cultivars. Furthermore, data pertaining to seed weight per plant {11.47 (TKG-22) to 16.23 g (swetha til)} and harvest index {13.1

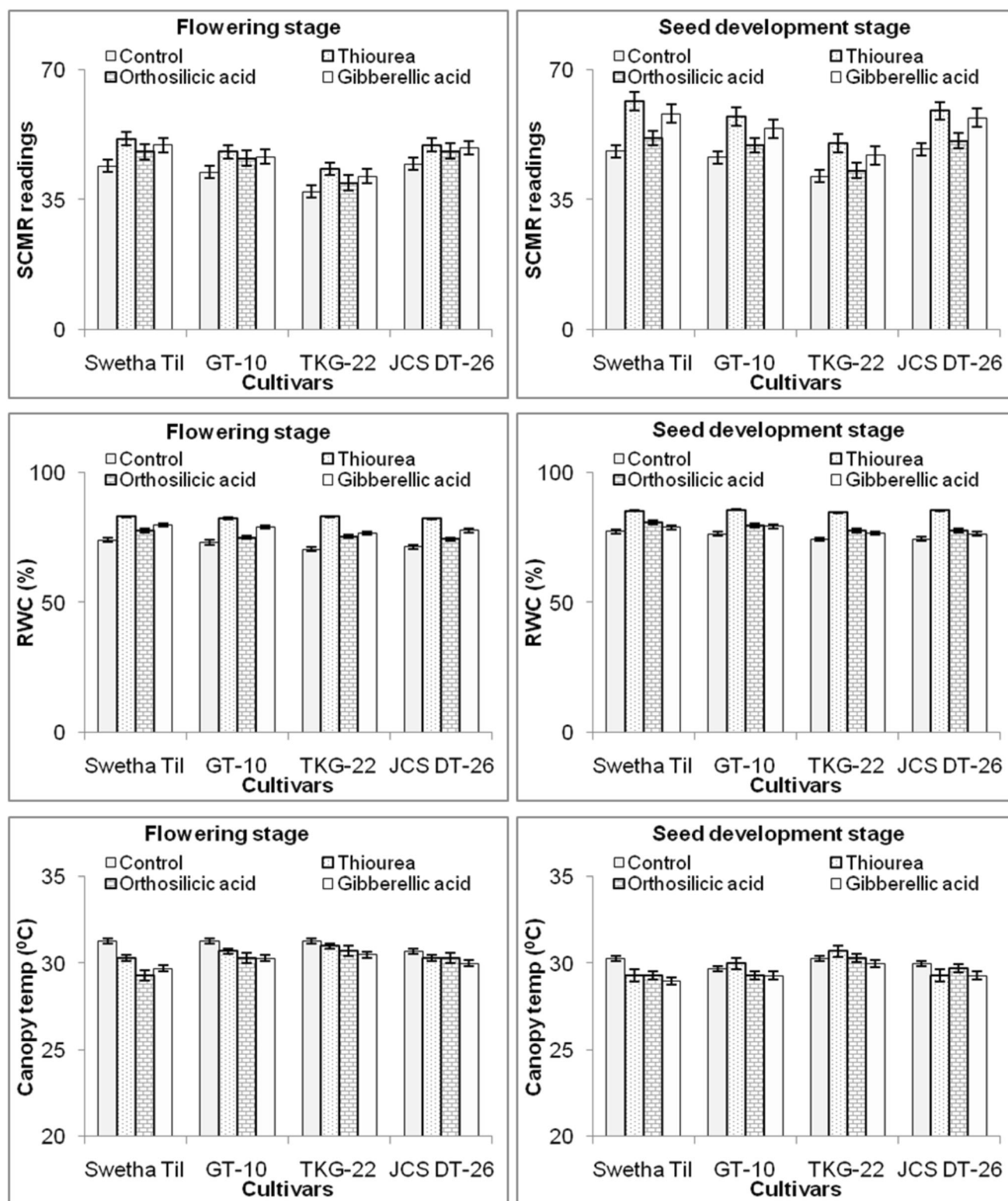


Fig. 2 Effect of different PGRs on physiological traits (SCMR: SPAD chlorophyll meter readings, reading, RWC: relative water content and canopy temperature) at flowering and seed development

stage among sesame cultivars. Data are the means of five replicated plants for each cultivar ($p < 0.05$)

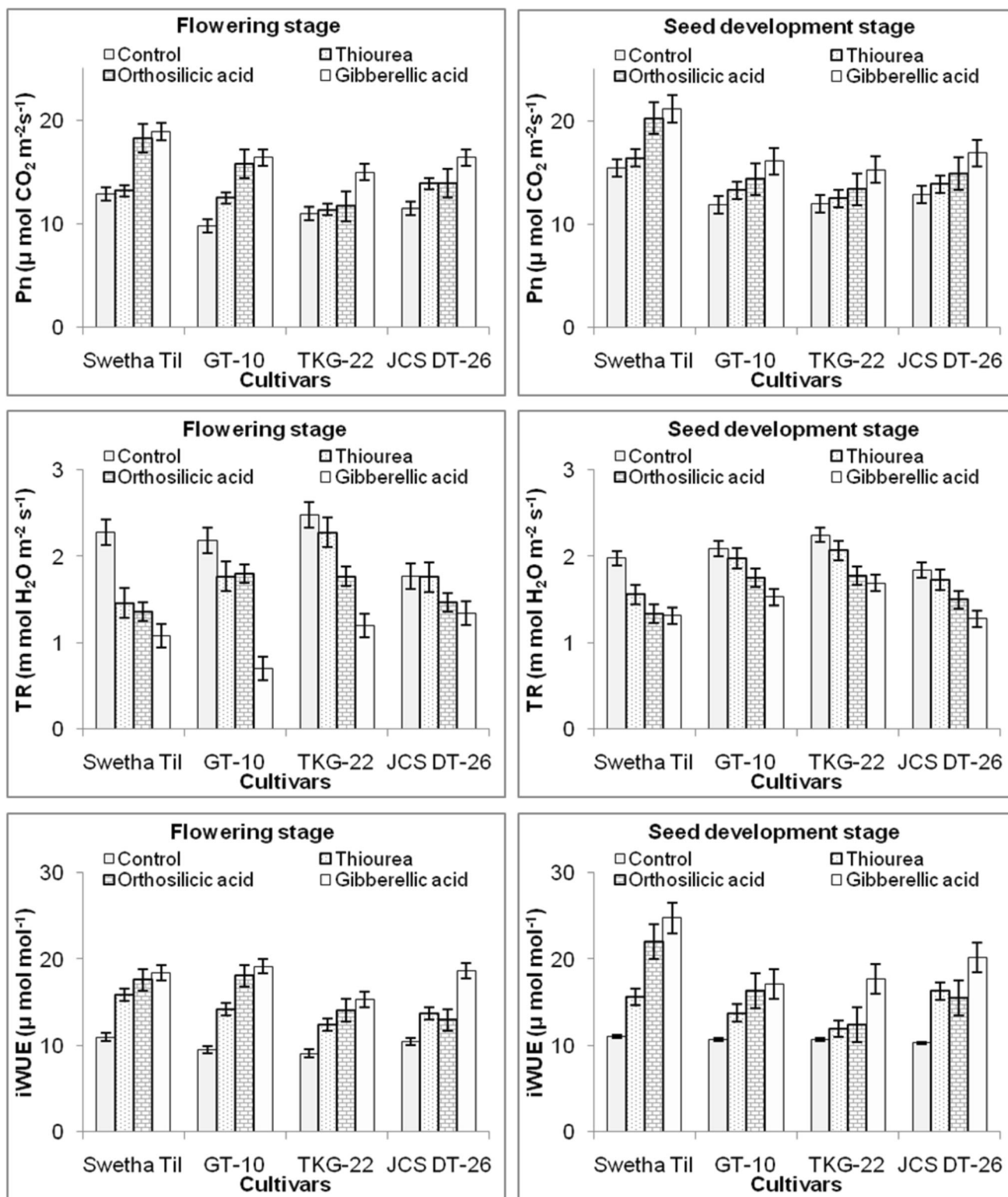


Fig. 3 Effect of different PGRs on physiological traits (Pn: photosynthetic rate, TR: transpiration rate and iWUE: intrinsic water use efficiency) at flowering and seed development stage among sesame cultivars. Data are the means of five replicated plants for each cultivar ($p < 0.05$)

(TKG-22) to 23.0% (swetha til)} showed significant differences (Fig. 4). The percent increase calculations indicated that the application of all three PGRs, viz., GA3

(25–26%), OSA (10–11%), and TU (6–7%), significantly enhanced the seed yield in sesame and among the cultivars.

Table 1 Influence of plant growth regulators (TU: 500 ppm; OSA: 380 ppm; GA₃: 20 ppm and C: water sprayed) on seed yield/plant, harvest index and oil content traits of sesame (varieties-V1: Swetha Til; V2: GT-10; V3: TKG-22 and V4: JCSDT-29) at flowering stage and seed development stage

Treatments	Seed yield/plant (SYP)					Harvest index (HI)					Oil content (OC)				
	V1	V2	V3	V4	M	V1	V2	V3	V4	M	V1	V2	V3	V4	M
Control	12.57	11.73	11.47	12.00	11.9	19.5	16.5	13.1	17.4	16.7	42.2	41.6	43.3	45.9	43.3
GA ₃	16.23	14.27	14.23	15.03	14.9	23.0	20.3	19.5	22.0	21.2	49.8	48.6	48.5	49.5	49.1
OSA	14.47	12.80	12.83	13.10	13.3	21.4	19.0	17.8	20.3	19.6	49.2	49.0	48.1	49.2	48.9
TU	13.57	12.13	12.53	12.70	12.7	20.2	17.7	16.1	18.3	18.1	49.3	49.2	48.0	49.0	48.9
	S. Em ±		CD (5%)			S. Em ±		CD (5%)			S. Em ±		CD (5%)		
Varieties	0.06		0.17			0.08		0.22			0.42		0.82		
PGRs	0.06		0.17			0.08		0.22			0.42		0.82		
Interaction	0.11		0.33			0.15		NS			0.84		1.64		

T₁ treatment, M mean, significance level: 5% level

Among the cultivars, the highest seed yield was observed in cv. swetha til followed by JCSDT-29 (Fig. 5).

Effect of PGRs on Biochemical Traits

Sesame oil is legendary for its stability as a result of its oxidation resistance; it is also a rich source of saturated and unsaturated fatty acids. The oil content among sesame cultivars ranged from 41.6 (GT-10) to 49.8% (swetha til). With respect to oil content, it was reported that the foliar application of GA₃ was most promising in improving the oil content, followed by TU and OSA. The GA₃ increased the oil content by almost 13.4%, whereas both OSA and TU enhanced the oil content by almost 12.9% among sesame cultivars. The highest oil content was recorded in cv. JCSDT-29, followed by swetha til, which had the maximum oil content of GA₃ (Supplementary Table 5 and Fig. 4). Results showed that both saturated (palmitic acid) and unsaturated (oleic and linoleic acid) fatty acids were improved upon the application of PGRs. The palmitic acid varied from 8.2 to 11.6%, the oleic acid from 42.4 to 49.8%, and the linoleic acid from 33.7 to 42.8%. It was reported that application of GA₃ followed by OSA was most effective in improving the both saturated and unsaturated fatty acids in sesame, whereas among the cultivars, swetha til was performed superiorly compared to the rest of the cultivars and control.

Discussion

The sesame cultivation is mostly restricted to the arid/semi-arid regions. Maintaining the yield potential of sesame genotypes through the application of different PGRs is an

important avenue of research to enhance productivity under rainfed conditions. The improvement in plant's resistance to the different stresses, together with drought stress results in accelerated growth and development processes [7]. In the present study, an apparent relationship between PGRs and growth parameters has been established in sesame. It was observed that the application of PGRs not only improved plant growth by regulating the plant's physiological processes but also significantly contributed to enhanced seed yield (almost 25–26%) in sesame under rainfed conditions. The recent findings suggested that crop growth and physiological parameters can be used for the estimation of plants' ability to withstand adverse climatic conditions [2–4, 51, 62, 74]. A remarkable increase in total leaf area (72–74%), plant height (30–50%), and the number of branches (9–10%) was observed due to the application of GA₃ followed by TU and OSA as compared to control. The application of GA₃ might have aided in cell elongation and turn stem elongation, by increasing the wall plasticity and consequently [16] improving the growth traits [37, 79]. In addition, increased leaf area due to application of GA₃ captured more light which ultimately results in enhanced plant's dry weight [34].

The application of PGRs enhanced the trait expression under rainfed conditions among cultivars tested. Earlier reports suggested that the limited water availability during crop growth drastically reduced the physiological trait expression in sesame [4, 51, 67, 75]. Results indicated that the SPAD values an index of the pigment chlorophyll are essential to harvest photons [13]. Our results showed that the SPAD values in tested varieties were increased by 14–15% at flowering and 23–24% at the seed development stages upon application of TU under rainfed conditions. The enhancing effect of TU on SPAD values was due to the

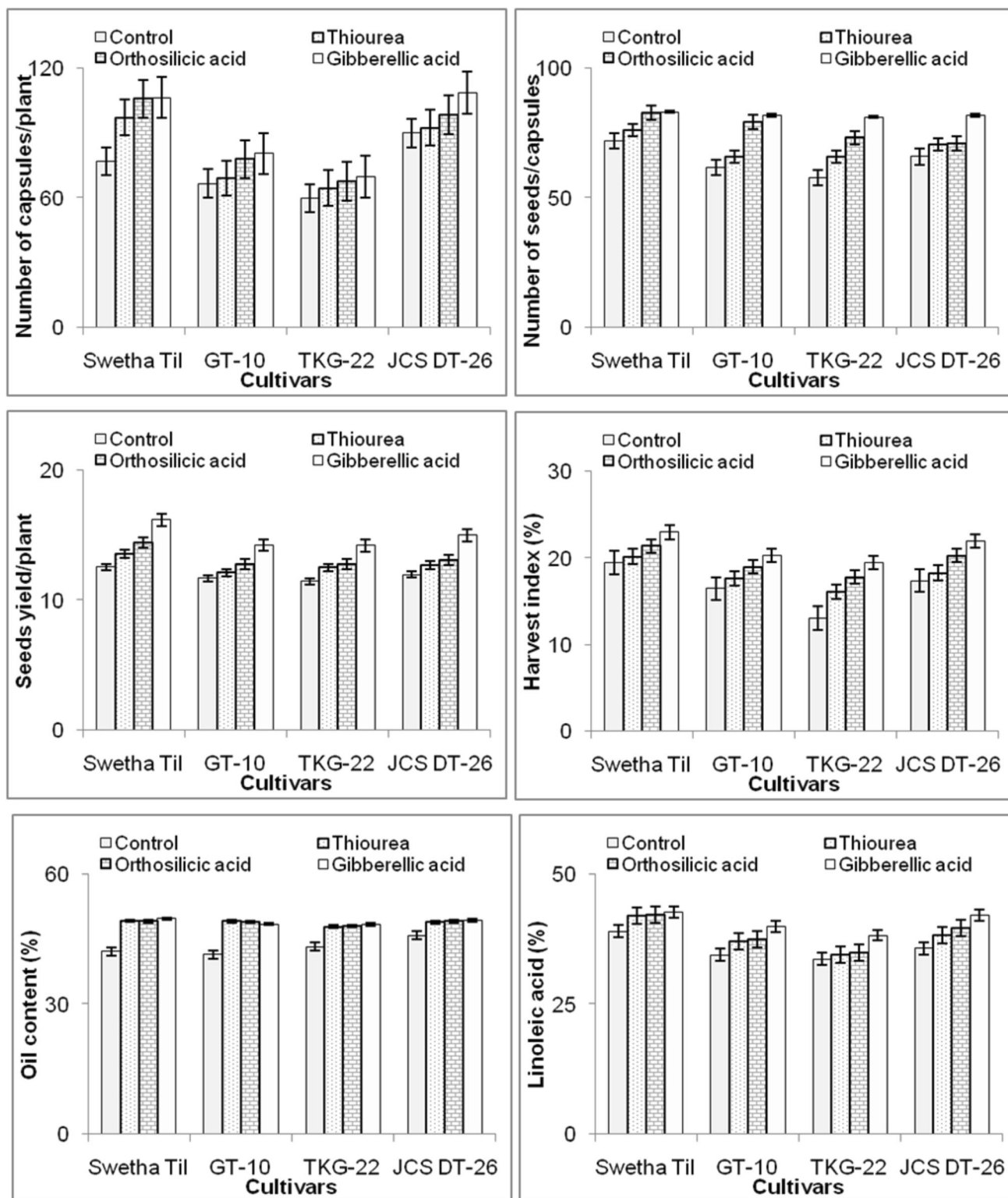


Fig. 4 Effect of different PGRs on yield contributing, yield and biochemical traits (number of capsules/plant, number of seeds/capsule, oil content and linolenic acid) among sesame cultivars. Data are the means of five replicated plants for each cultivar ($p < 0.05$)

presence of 'amine' and 'thiol' group that probably act as a ROS (reactive oxygen species) scavenger or maybe supplier of nutrients under water-limited conditions

[52, 54, 60, 76]. Moreover, the application of TU improves the photosynthesis efficiency, which is strongly linked with the up-regulation of genes related to large subunits of

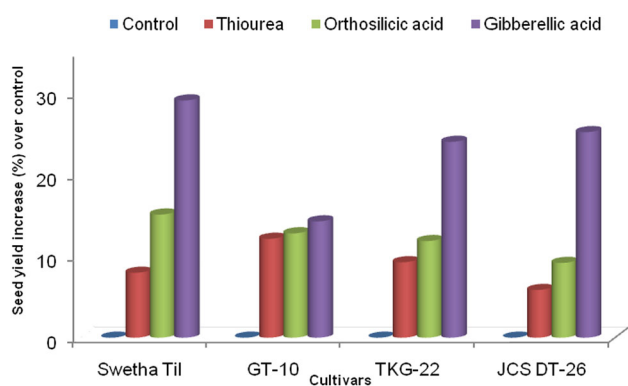


Fig. 5 Percent increase in seed yield due to application of different PGRs among the sesame cultivars. Data are the means of five replicated plants for each cultivar ($p < 0.05$)

Rubisco that protect the photosynthetic assembly under water-limited conditions. This corroborates the views of Vineeth et al. [81].

Another important trait under water-limited conditions is leaf tissue relative water content, an indirect measure of tissue water status since even mild water stress has been reported to affect the RWC [4, 20, 50, 51]. Our results indicated that the application of different PGRs, particularly TU significantly improves the RWC (13–15%) in sesame cultivars under rainfed conditions. These results are in good agreement with the findings of Akladios et al. [1] in sunflower. During the early plant growth and developmental stages, limited water availability impairs the biosynthesis of chlorophyll, ceases the rate of photosynthesis and relative water content, and ultimately results in lower seed yields [14]. Thiourea plays an essential role in plant growth, development, and yield formation [47, 89]. The application of TU under water-limited environments brings down the water consumption by plants [83] and enhances the water use efficiency [21].

Previous studies revealed that moisture stress negatively affects the photosynthetic rate and other related parameters in sesame [22, 23, 66, 75, 85]. Similar to this, water-limited conditions restrict all photosynthesis-related parameters of sesame in the present study. However, results indicated that the application of GA_3 followed by OSA and TU significantly improved the photosynthetic rate and other related traits as compared to the control. These results are found in well accordance with the findings of Behera et al. [10] in sesame. Yuan et al. [87] suggested that foliar application of GA_3 promotes the development of chloroplasts by promoting the levels of protochlorophyllide oxidoreductase (POR) [69], prolonged chlorophyll synthesis, stimulates the Rubisco activity [46], and subsequently, photosynthetic efficiency which contributes to improved physiological activity. Khan et al. [32, 35] reported that the application of GA_3 significantly increased the photosynthetic rate in

mustard which is due to enhanced activity of the carbonic anhydrase enzyme. The enzyme carbonic anhydrase helps maintain a constant supply of CO_2 to Rubisco and also plays a crucial role in photosynthetic CO_2 fixation in the stroma [78]. On the other hand, the role of TU in improving photosynthetic efficiency and maintaining redox homeostasis through its broad range of ROS scavenging activity has been already established [31, 81]. Application of silicon particularly at higher concentrations enhanced water uptake, transpiration rate and stomatal conductance in plants [15]. Silicon helps in maintaining an optimum CO_2 levels for photosynthesis and prevents photo-inhibition under water deficit conditions. Zhang et al. [90] revealed that silicon promotes the transcription of some photosynthesis-associated genes, improves the photochemical process, and consequently enhances the process of photosynthesis.

Apart from the soil moisture, the atmospheric temperature is the other climatic variable that has a great influence on germination, growth, capsule formation [38] and yield of sesame [57]. No doubt, cultivars with lower canopy temperatures secured higher yields as reported in other studies [10, 41, 51]. Due to the importance of evaporative cooling as a major component of the leaf energy balance, leaves temperature can be used as an indicator for rates of water loss or stomatal opening. Our results showed that the application of PGRs significantly lowered the CT and increased the stomatal conductance. The cv. Swetha til had minimum canopy temperature and higher stomatal conductance when treated with GA_3 , followed by OSA, and TU. Application of GA_3 increased the number of stomata, dimension of stomata, and stomata pore size [28]. Water uptake is crucial for seed yield in any crop [41, 64, 65]. Under water stress conditions, a plant's ability to control the size of the stomatal opening is an important mechanism to control water loss. Alongside, Goring [24] stated that the increased stomatal conductance due to the application of GA_3 has been related to the higher accumulation of carbohydrates and potassium in guard cells of treated plants that may influence the speed and degree of stomata opening. Hence, by maintaining a favorable water uptake and controlling the stomata size, opening and closing of stomata and stomatal conductance plants tend to regulate leaf temperatures. In addition, the role of OSA in maintaining leaf water status by closing stomata, increasing relative water content and cell turgor pressure under water deficit conditions was also established in previous studies such as Ratnakumar et al. [59] and Wakchaure et al. [83, 84]. Therefore, it can be concluded that these surrogate traits such as SCMR, RWC, and CT greatly contributed to the enhancement of final seed yield with the application of PGRs.

In sesame, seed yield is a complex trait that depends upon several yield-contributing traits. The results suggested that yield-contributing traits such as NCP, CWP, NSC, TW, TDM, and SWP were improved due to the application of PGRs. Among the different PGRs tested, GA₃ followed by OSA was found most superior and improved all the yield-contributing traits including seed yield compared to the control and rest of the PGRs. The per se performance revealed that NCP by almost 24–25%, NSC by 27–28%, seed yield by 33–34%, and harvest index by 26–27% increased with the application of GA₃ and these results are in corroboration with the reports of Khan et al. [33, 34] in mustard; whereas Vekaria et al. [22], Hadif [24], and Thuc et al. [79] in sesame. Application of GA₃ improves the plant's fruit-set ability, increases the number of fruits [55], reduces fruit shattering and enhances translocation of photo assimilates to seeds [33] in mustard. In addition, foliar application with GA₃ probably contributed to seed formation, and their optimum nourishment, and reduced the number of aborted seeds [12]. During the grain-filling stage, GA₃ has a positive role in promoting the development of embryos that subsequently results in grain-filling process, and an increase in mean grain weight [87]. GA₃ improves the weight of seeds compared to control but the observed difference was not significant, indicating GA₃ is not very effective in improving seed mass. On the other hand, Silicon was also proven to enhance economic yields in crop plants by modifying the mobilization of photo assimilates source-sink relationships, increasing photosynthesis, conductance of mesophyll cells, nutrient use efficiency from vegetative tissues to reproductive organs [18, 19].

Sesame is known for its superior oil quality and the results of the current study suggested that GA₃ (20 ppm) application is highly promising in improving the oil content and quality traits (saturated and unsaturated fatty acid) of seeds. Foliar application of GA₃ improved the oil content by almost 13–14% in sesame and these results are found in agreement with the reports of Aytac and Kinaci [5] and Nizamani et al. [49] in Brassica. The fatty acid profiling showed that the application of GA₃ significantly influenced both saturated (palmitic acid) and unsaturated (oleic and linoleic acid). Treatment with GA₃ at 20 ppm increased the palmitic acid by almost 23–24%, oleic acid by around 12–13%, and linoleic acid by nearly 13–14% in sesame cultivars. However, the variation among the cultivars for both oil content and fatty acid contents was not much higher. These findings are in agreement with the reports of Ijaz et al. [29] on canola, and Hamza [26] on safflower. The

foliar application of GA₃ can be attributed to the enhanced synthesis of enzymes that are directly associated with the synthesis of and metabolisms of fatty acid [16, 17].

Conclusions

The exogenous foliar application of PGRs has significantly improved the morphological, physiological, total seed yield, and quality traits such as oil and fatty acid content in the sesame cultivars tested. Most of the traits responded better with the application of gibberellic acid (20 ppm), followed by ortho-silicic acid (380 ppm) and thiourea (500 ppm). Swetha til, a white-colored cultivar followed by JCSDT-29 were registered superior morpho and yield attributes for most of the traits studied; whereas thiourea was found highly effective in improving the physiological traits. The enhanced seed yield was 25–26%, 10–11%, and 6–7% recorded with the application of gibberellic acid, ortho-silicic acid, and thiourea over control. Based on various trait responses, it can be concluded that the foliar application of gibberellic acid at 20 ppm is recommended for optimum productivity under rainfed conditions for the sesame variety swetha til.

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Data availability Access to cultivar resequencing data can be obtained by contacting the corresponding author. All other datasets generated and analyzed for this study are included in the article/ Supplementary Material.

Declarations

Conflict of interest The authors do not have any conflicting interests.

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