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RESEARCH ARTICLE

Improving source-sink relationship and harvest index through assimilate partitioning in sunflower (*Helianthus annuus* L.)

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Abstract

Sunflower (*Helianthus annuus* L.) production in India is constrained by its cultivation on marginal, nutrient- and moisture-deficient lands. This study aimed to enhance sunflower productivity by improving assimilate partitioning efficiency and source-sink relationships. This shows common limitations of low harvest index (HI) and inefficient nutrient allocation in the sunflower crop. Hence, the experiment was conducted at Zonal Agricultural Research Station (ZARS), University of Agricultural Sciences (UAS), Gandhi Krishi Vigyana Kendra (GKVK), Bangalore, during kharif and rabi seasons of 2022 and 2023 to evaluate modifications in source–sink relationship and assimilate partitioning for enhancing HI in sunflower. The experiment consisted of 9 treatments, tested in a randomized complete block design and replicated thrice using sunflower hybrid KBSH-44. The results revealed that among the different treatments, the application of 3000 ppm chlormequat chloride (cycocel) and double nitrogen (N) at sowing, combined with a micronutrient mixture at the ray floret stage, consistently outperformed others across seasons. These treatments notably increased plant height, leaf area index, crop growth rate, seed filling percentage and final seed yield. Defoliation treatments provided valuable insights into the plant's ability to redistribute assimilates under reduced source conditions, demonstrating compensatory mechanisms within the crop. The study highlights the importance of integrating plant growth regulators (PGRs), precise nutrient management and strategic canopy modifications to enhance source-sink efficiency and overall productivity in sunflowers.

Keywords: assimilate partitioning; canopy management; cycocel; harvest index; plant growth regulators; sunflower

Introduction

Sunflower (*Helianthus annuus* L.) is one of the most important vegetable oilseed crops and is native to the southern parts of the USA and Mexico (1). It is popular due to its high-quality edible oil and wide adaptability to diverse environments. It is largely cultivated under rainfed conditions during the kharif season and in residual soil moisture during the post-rainy season, i.e., rabi and summer season. The importance of sunflowers in the annual oilseed scenario has increased considerably in recent years (2).

In India, sunflower cultivation is predominantly concentrated in the southern states, including Karnataka, Andhra Pradesh and Tamil Nadu, which together contribute over 70 % of the national production. Other important sunflower-growing areas include parts of Maharashtra and Rajasthan (3). These regions are characterized by semi-arid to dry climates where sunflower serves as a vital oilseed crop adaptable to moisture stress conditions. Sunflower is becoming popular because of its wider adaptability to different agro-climatic zones and soil types, easy crop management, photo-insensitivity, short duration, high seed multiplication ratio and higher oil percentage in the seed. The day-neutral nature of this crop enables its cultivation around the year and is increasingly integrated in newer agroecological niches and cropping systems. However, its productivity remains limited by several physiological and environmental constraints, including inefficient assimilate partitioning and poor source-sink dynamics. The source-sink relationship, which determines the translocation and partitioning of photosynthates from source tissues (mainly leaves) to sink tissues (seeds and pods), is a critical factor influencing crop yield and HI (4).

Approximately 95 % of the dry matter in plants originates from photosynthesis (5). Therefore, optimizing the photosynthetic capacity and enhancing the translocation of assimilates towards sink tissues (seeds) is essential for improving oilseed productivity. Various strategies have been explored to enhance source-sink relationships in crops, including carbon dioxide enrichment, foliar application of nutrients and chemical agents like sodium bisulfate and enhanced nitrogen (N) availability (6, 7). Among these, the use of plant growth regulators (PGRs) and canopy management has emerged as effective approaches to modulate plant function, improve nutrient use efficiency and strengthen source-sink dynamics (8). Partitioning of assimilates among plant organs is primarily determined by the translocation dynamics of photosynthates, which is often expressed in terms of the partitioning coefficient or harvest index (HI). A higher translocation rate of photosynthates toward the sink tissues results in increased productivity (9). Moreover, strategic canopy management, including defoliation and thinning influences light interception, transpiration efficiency and water use efficiency, thereby improving the source-sink balance (10). Modifying assimilate partitioning as a contingency strategy holds significant promise for oilseed crops under moisture stress conditions. For example, assimilates produced during the pre-anthesis stage can be redirected towards seed filling when moisture stress occurs during the reproductive phase (11). Stress-induced changes in assimilate partitioning, if appropriately managed, could enhance reproductive growth and ultimately improve yield (12). Hence, this study was undertaken at the University of Agricultural Sciences (UAS), Bangalore, to evaluate modifications in source–sink relationships and assimilate partitioning for enhancing the HI in sunflower.

Materials and Methods

Experimental design and planting material

The field experiment was conducted during the kharif and rabi seasons of 2022 and 2023 at ZARS, UAS, Bangalore, using KBSH-44 hybrid. The research station is geographically located at 12°58' N latitude and 77°35' N longitude at an altitude of 930 m above mean sea level (air temperature: maximum- 31 °C, minimum- 13 °C). The soil of the experimental field is red lateritic soil with neutral soil pH (6.86), medium in available N (297.5 kg ha^{-1}), phosphorus (P) (34.20 kg ha^{-1}) and potassium (K) (34.20 kg ha^{-1}). The experiment was laid out in a randomized complete block design with 3 replications. Farmyard manure (10 t ha^{-1}) was uniformly applied to each plot 3 weeks before sowing. Basal application included 50 % N and 100 % phosphorus pentoxide (P_2O_5) and potassium oxide (K_2O), supplied through urea, single superphosphate and muriate of potash. The remaining 50 % of N was applied at 30 days after sowing (DAS) in the form of urea and earthing up was carried out. The crop was sown during the last week of July and harvested when the capitulum seeds were completely dried. Five plants were randomly sampled from each net plot for recording growth and yield parameters.

Treatment details

Plants were subjected to the different treatments designed to influence source-sink dynamics (Table 1).

Measured parameters

Morphological parameters

Plant height was measured as the distance from the base of the plant to its apex (in cm), the number of leaves was calculated taking into account the total count of leaves per plant at the harvest and total plant leaf area measured using a leaf area meter. The Soil Plant Analysis Development (SPAD) chlorophyll meter reading (SCMR) was measured using a SPAD chlorophyll meter (Minolta SPAD-502). The leaf area duration (LAD) and leaf area index (LAI) were calculated using the formula:

Leaf area index (LAI)

$$\text{LAI} = \frac{\text{Leaf area per plant (cm}^2)}{\text{Spacing}}$$

Leaf area duration (LAD)

$$\text{LAD} = \frac{\text{LAI}_1 + \text{LAI}_2 \text{ x } (t_2 - t_1)}{2}$$

Where,

LAI_1 = Leaf Area Index measured at time t_1

LAI_2 = Leaf Area Index measured at time t_2

t_1= time (or date) of the first LAI measurement

t_2= time (or date) of the second LAI measurement

Biomass and dry matter parameters

During the harvest, roots, leaves, stems and flower heads were separated. All plant parts were oven-dried to constant weight at 70 ° C. Dry weights of root, stem leaf and head were recorded and total dry matter (TDM) was calculated as the sum of part dry weights of root, stem, leaf and head.

Yield parameters

Seed filling percentage (%) was obtained by formula: (Filled seeds / Total seeds) × 100. The 100-achene weight (test weight) obtained by measuring the weight of 100 seeds (g), total number of seeds per plant (count of all seeds per head), head diameter (diameter of the capitulum in cm), HI = (Seed yield / TDM) × 100, seed yield (g ha^{-1}) and oil content were analyzed. Oil content was determined using a Nuclear Magnetic Resonance (NMR) instrument. Yield parameters were recorded after harvest.

Statistical analysis

Analysis of variance (ANOVA) and Tukey HSD were performed using Statistical Package for Social Sciences (SPSS) v26. software and line graphs for various traits, correlation studies were performed using GraphPad Prism v10. The spider plot and dual-axis combination chart were generated using the SR plot.

Results

Effect of different treatments on various morpho-physiological parameters in sunflower across seasons

Growth attributes such as plant height, number of leaves per plant, LAD, total leaf area, LAI, SPAD readings and TDM differed significantly among treatments. However, days to physiological maturity and chlorophyll content were non-significant during both kharif and rabi seasons (Fig. 1). Application of double dose of N at sowing and micronutrient mixture at ray floret stage (T8) recorded significantly higher plant height (190 and 176 cm), number of leaves plant^{1} (39 and 38), LAD (63.35 and 59.98), total leaf area (10854 and 11466 cm^2

Table 1. Details of treatments used in the experiment

Treatment code	Treatment description
T1	Control (as per the standard package of practices)
T2	Spraying of TIBA (240 ppm) + NAA (120 ppm) at the ray floret stage
T3	Spraying of boron (0.2 %) at the ray floret stage
T4	Removal of basal leaves (33 % of total leaves) at the ray floret stage
T5	Removal of middle leaves (33 % of total leaves) at the ray floret stage
T6	Application of nitrogen (60 kg ha^{-1}) at the star bud stage
T7	Foliar application of humic acid (8 %) at 60 and 75 DAS (2 sprays)
T8	Double dose of nitrogen at sowing + micronutrient mixture (boron and zinc at 0.2 %) at ray floret stage
T9	Application of benzyl adenine (150 ppm) at the ray floret stage (2 sprays during the seedling and grain-filling stages)
T10	Spraying of cycocel (3000 ppm) at the star bud stage

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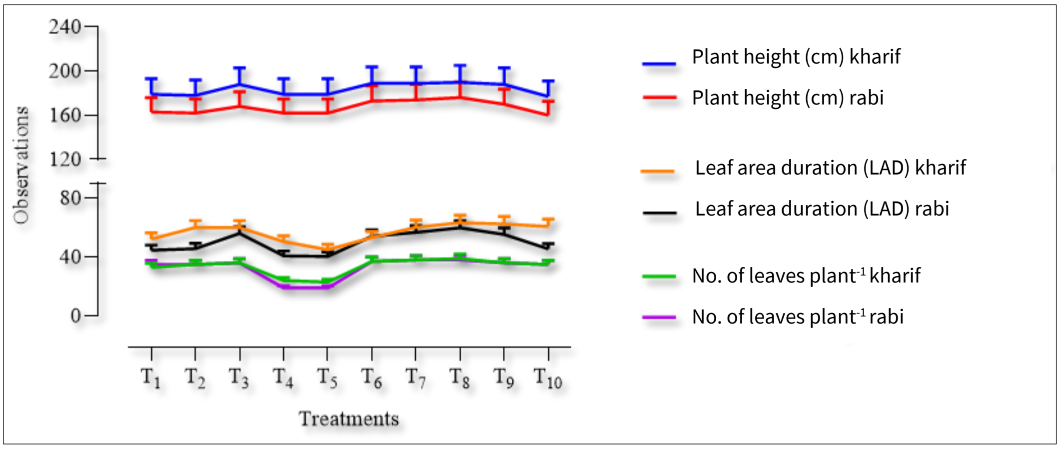

Fig. 1. Line chart showing the influence of source and sink manipulations on plant height, number of leaves and leaf area duration at 60 DAS in sunflower during kharif and rabi seasons.

plant^{-1}), LAI (6.03 and 6.37) and SPAD reading (44.0 and 43.61). It was on par with foliar application of humic acid 8 % at 60 and 75 DAS (T7) (plant height–189 and 174 cm, number of leaves plant^{-1}–38 and 38, LAD-60.36 and 56.81, total leaf area-9972 and 9594 cm^2 plant^{-1}, LAI-5.54 and 5.33 and SPAD reading-43.5 and 43.55). N application at star bud stage at 60 kg ha^{-1} (T6) recorded plant height (189 and 173 cm), number of leaves plant^{-1} (37 and 37), LAD (53.16 and 54.09), total leaf area (10584 and 7004 cm^2 plant^{-1}), LAI (5.88 and 5.28) and SPAD (43.4 and 43.28). However, significantly lower plant height was observed with foliar spray of chlormequat chloride (cycocel) at 3000 ppm at the star bud stage (T10) (plant height-177 and 160 cm, number of leaves plant^{-1}-35 and 35, LAD-60.84 and 45.56, total leaf area-9342 and 9288 cm^2 plant^{-1}, LAI-5.19 and 5.16 and SPAD reading-44.4 and 44.2) (Fig. 2).

Role of growth regulators and nutrients in seed setting and filling

Seed setting and seed filling problems are among the primary constraints in sunflower production and are often considered major reasons for low productivity. Plant growth regulators (PGRs) influence all stages of plant growth, from germination to maturity, by modifying hormonal balances. These natural or synthetic hormones can regulate processes like seed development and seed filling. In the study, 3000 ppm cycocel (T10) significantly improved seed filling in both kharif and rabi, followed by T9 (150 ppm benzyl adenine). Other effective treatments included 0.2 % boron (B) (T3), double N at sowing with micronutrient mixture (T8) and 2,3,5-Triiodobenzoic acid (TIBA) with naphthaleneacetic acid (NAA) spray (T2). In contrast, defoliation treatments (T4: basal leaves, T5: middle leaves) severely reduced seed filling, underlining the importance of source leaves (Table 1 and Fig. 3).

Impact on yield attributes and seed oil content

Yield attributes such as 100-achene weight, seed yield per plant, number of seeds per head and oil content were markedly improved with the application of growth regulators. In kharif, the maximum 100-achene weight (6.22 g) was recorded in T10, followed closely by T9 and T2. These increases were attributed to better translocation of photosynthates and improved source-to-sink dynamics due to plant size management. Spraying 0.2 % B and other PGRs increased both achene number and weight. T10 also recorded the highest seed yield per plant, with notable contributions from increased head diameter, seed filling, seed count and achene weight. Other effective treatments included T9 and T2 (Fig. 4). Cycocel was especially effective in reducing plant height, thus improving resource translocation efficiency (12).

The increased seed yield could also be attributed to the higher dry matter production and its accumulation in reproductive parts, chlorophyll content, higher number of filled seeds, head diameter, high seed filling percentage and 100-seed weight (13). Oil content was significantly affected across treatments. The significantly highest oil content (34 %) was observed in T10, on par

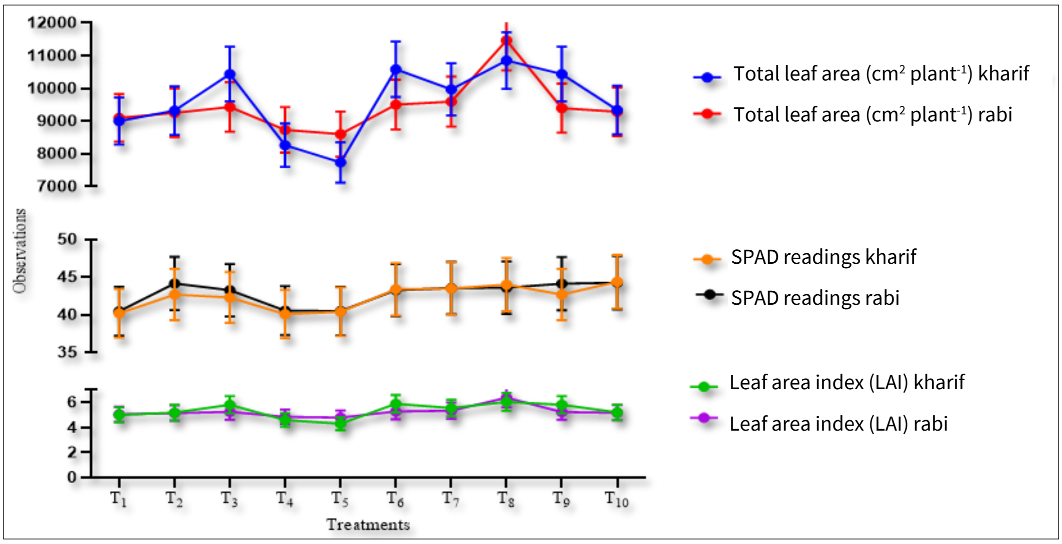

Fig. 2. Line chart showing the influence of source and sink manipulations on total leaf area, leaf area index and SPAD readings at 60 DAS in sunflower during kharif and rabi seasons.

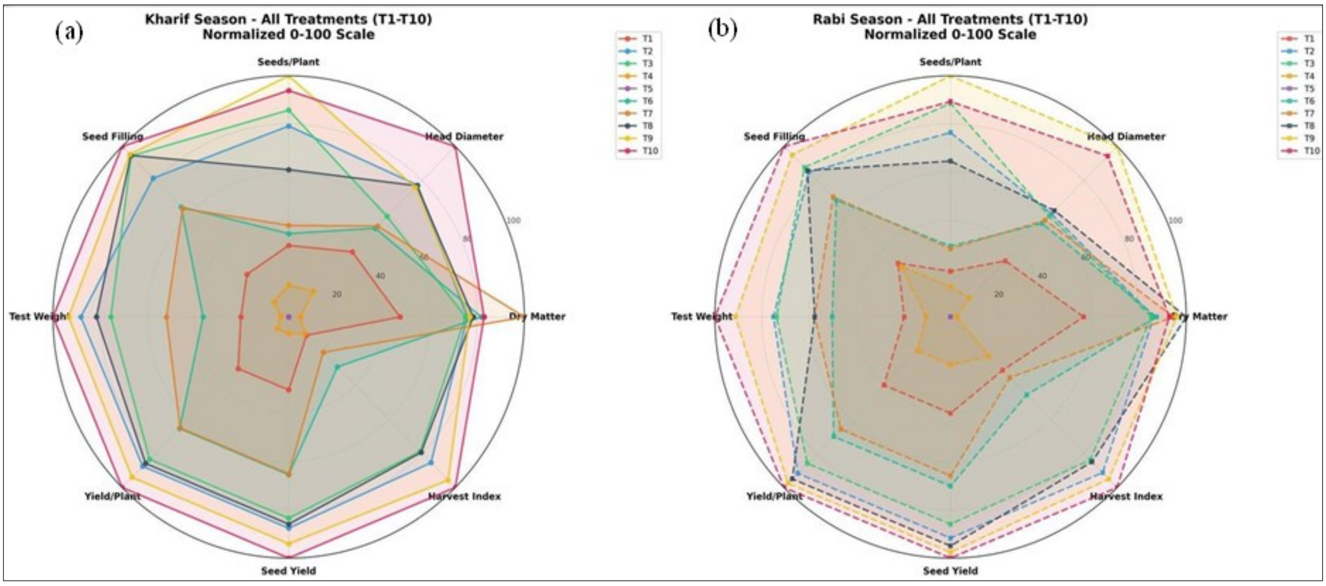

Fig. 3. Spider plots showing effects of different treatments on yield parameters in sunflower.

with T8, while the lowest was recorded in T5. Micronutrient application played a role in improving oil biosynthesis and enzyme activity. Increased yield and oil content were positively correlated with dry matter production, chlorophyll content, crop growth rate (CGR) and seed parameters (Fig. 4) (14).

Source-sink relationships, biomass partitioning and harvest index

Plant treated with a double dose of N along with micronutrient application (T8) resulted in maximum LAD, which was 33.8 % more than the control, whereas the least LAD was recorded when extra N was applied at the star bud stage (10). Maximum seed yield was recorded when the plants were sprayed with (3000 ppm) cycocel due to a higher photosynthetic rate (4.6 % increase); however, it did not influence LAD significantly. In addition, foliar application of humic acid and application of benzyl adenine also increased seed yield (46.8 and 48.6 g plant^{-1} respectively), which increased HI. When the source size was reduced by removing basal leaves (T4) and middle leaves (T5) at the ray floret stage, yield was affected significantly due to a reduction in functional leaf area and thus the photosynthetic rate (15) (Table S1).

In addition to all these treatments, sink capacity was also manipulated by spraying TIBA (240 ppm) with NAA (120 ppm) and 0.2 % B was sprayed at the ray floret stage to improve the rate of translocation (16). These 2 treatments increased the yield by 33–36 %. The HI was also increased by 32 % due to more biomass and yield. Among all these treatments, spraying of 3000 ppm cycocel at the star bud stage increased seed yield significantly due to an increase in DM/LAD and the least yield was recorded when the source size was decreased by removing some leaves (16, 17). The overall result from this set of treatments indicated that there is a possibility of increasing yield up to 40 % either by increasing source size or by manipulating sink capacity, thereby improving translocation (18).

In general, increased source size (LAD) has significantly improved the seed yield by 32.6 % and the increase was highest in T4, followed by T10. Therefore, enlargement of source size is advantageous for yield improvement (1). Such yield improvement may be attributed to enhanced biomass or HI. B application likely enhanced assimilate demand at reproductive sinks, thereby increasing LAD (14). Differences in DM/LAD among treatments were

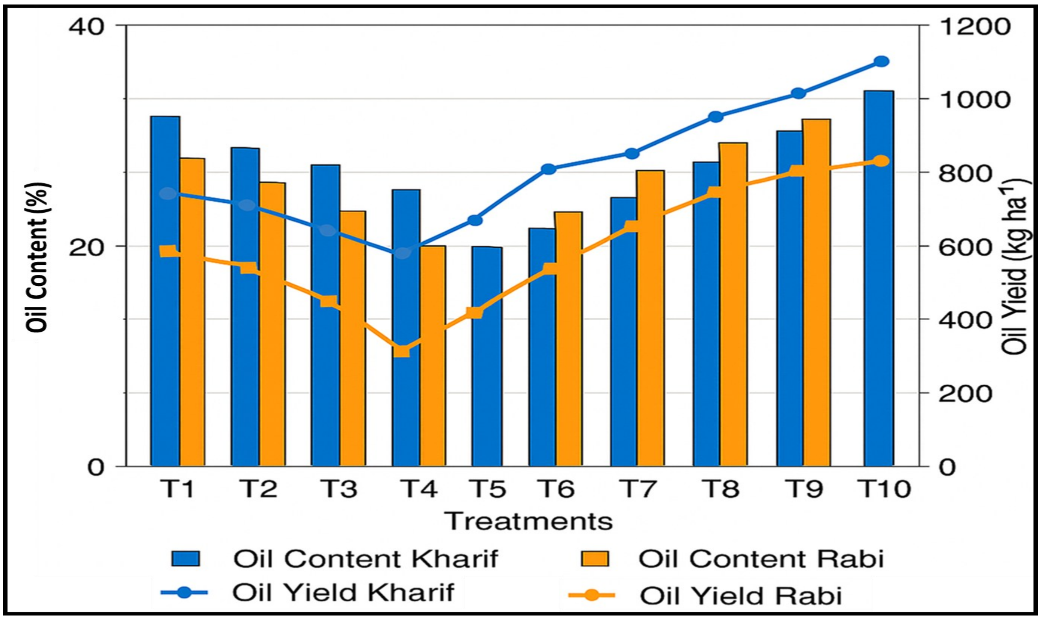

Fig. 4. Dual-axis combination chart showing the effect of different treatments on oil content and oil percentage in sunflower during kharif and rabi seasons.

negligible, suggesting that assimilation rate per unit leaf area is not a major constraint in sunflower. However, there is a significant difference between treatments for LAD (source size) (19). Therefore, strategies to enhance the leaf area would be useful to enhance the productivity of sunflowers to the extent of 30–40 % (6). An increase in LAD resulted in a 1.2 % increase in productivity. Among the strategies tried in general (including the literature), it would be optimum to go for T10 (application of 3000 ppm cycocel), if not possible, T9 (spraying 0.2 % B) may be utilized in sunflower production (Tables S2 and S3).

There is considerable scope for improving partitioning efficiency by restricting vegetative growth and increasing seed yield through foliar application of growth regulators such as cycocel (9). Applications of TIBA alone or TIBA with NAA have also been found to increase seed yield by 29 % and 34 % respectively. These results indicate that the translocation of metabolites from vegetative organs to the seed is a limitation for achieving HI (20). Any attempt to improve the transport of photosynthates from source to sink improves HI. The sink capacity seems to be a limitation for achieving high HI (19), therefore, by applying B or TIBA with NAA, sink capacity can be improved, leading to increased seed yield (HI)

The correlation matrix reveals strong positive relationships among growth, yield and oil traits, indicating that improved vegetative growth and reproductive performance significantly enhance overall productivity. TDM, head diameter and seed filling percentage showed the highest associations with seed and oil yield (Table 2). PC1 captured the overall productivity gradient (≈93 % variance) and is strongly associated with seed yield, oil yield, yield per plant, test weight, head diameter, seed filling, TDM and oil content (all load heavily on PC1). Treatments grouping on the same side of PC1 as these variable vectors (e.g., treatments such as T8–T10, T2, T3 depending on season) represent the high-productivity cluster, while defoliation treatments (T4, T5) plot on the opposite side and are associated with reduced productivity. PC2 (≈4.7 % variance) separates treatments with moderate differences in dry-matter and some season-specific responses (e.g., N and humic treatments), but contributes much less to the overall variation (Fig. 5).

Discussion

The present study revealed that cycocel and enhanced N application were the most effective treatments in improving sunflower growth and productivity under limited moisture conditions. The combination of growth regulators and nutrient management enhanced vegetative growth, yield attributes and oil content while minimizing the adverse effects of source limitation (18).

Table 2. Correlation matrix showing relationships among growth, yield and oil content parameters of sunflower (pooled mean of kharif and rabi seasons)

Parameter	TDM	Head diameter	Seed filling	Test weight	Yield/plant	Seed yield	HI	Oil content	Oil yield
TDM	1	0.88**	0.90**	0.84**	0.91**	0.91**	0.71*	0.97**	0.93**
Head diameter		1	0.96**	0.97**	0.97**	0.97**	0.91**	0.92**	0.97**
Seed filling			1	0.97**	0.99**	0.99**	0.93**	0.91**	0.99**
Test weight				1	0.97**	0.97**	0.96**	0.85**	0.97**
Yield/plant					1	1.00**	0.93**	0.93**	1.00**
Seed yield						1	0.93**	0.93**	1.00**
HI							1	0.76*	0.92**
Oil content								1	0.95**
Oil yield									1

*$p \leq 0.05$; **$p \leq 0.01$ (Pearson's correlation coefficients); TDM = Total dry matter; HI = Harvest index

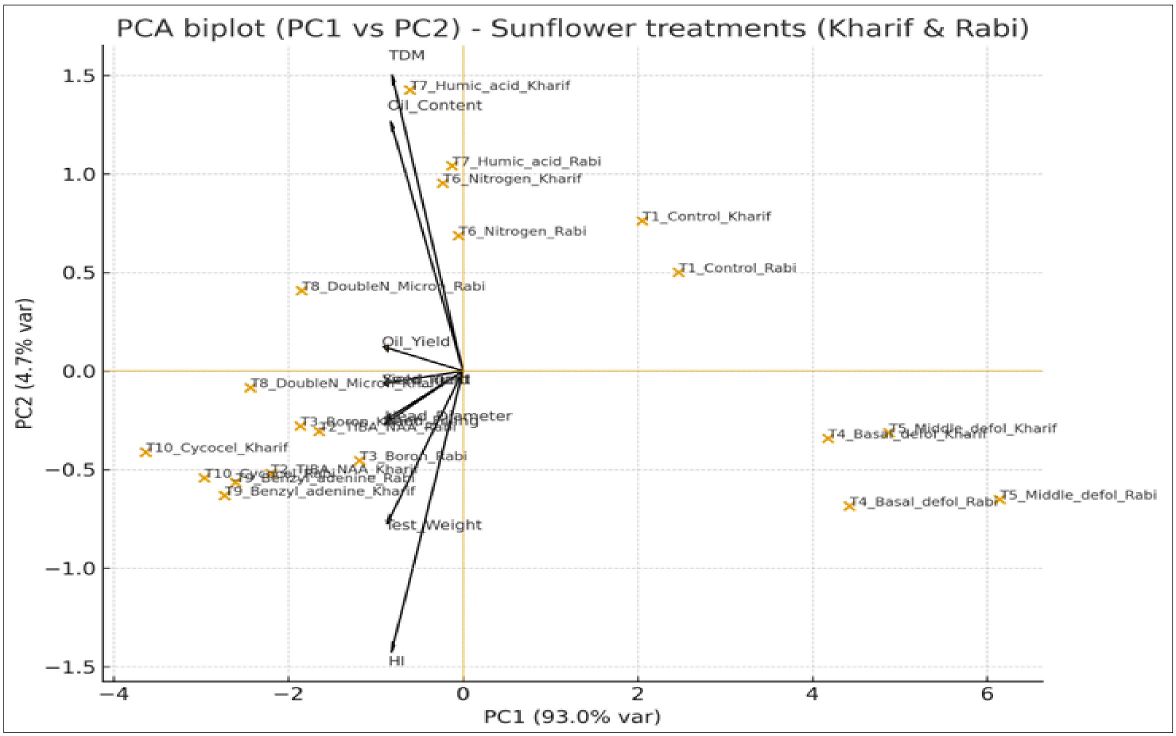

Fig. 5. PCA biplot showing trait associations and treatment grouping across kharif and rabi seasons in sunflower. Variance explained: PC1 - 92.98 %, PC2 - 4.69 %, PC3 - 1.02 % and PC4 - 0.71 %.

Plant height is largely a genetically controlled trait; however, several studies have demonstrated that it can be altered by N and growth regulator applications (13). In this study, application of a double dose of N at sowing with a micronutrient mixture at the ray floret stage increased plant height, followed by the application of 8 % humic acid and N at the star bud stage, which stimulated plant enzymes and hormones that improved soil fertility and nutrient uptake. This led to better growth attributes such as plant height, number of leaves, LAD, leaf area, LAI and SPAD values. Similarly, the application of micronutrients increased the crop growth rate, absolute growth rate and net assimilation rate in sunflower (14) (Fig. 2).

Cycocel and TIBA are anti-gibberellin agents, which inhibit gibberellin synthesis by blocking the conversion of geranyl pyrophosphate to copalyl pyrophosphate, the first step in gibberellin synthesis, thereby reducing excessive vegetative elongation and promoting compact growth (12, 16). Conversely, reductions in growth attributes with treatments like 3000 ppm benzyl alcohol, 150 ppm benzyl adenine and 240 ppm TIBA with 120 ppm NAA can be attributed to suppressed cell division and reduced cell expansion (15). These physiological responses reflect the typical mode of action of growth retardants, which limit excessive vegetative growth and redirect assimilates to reproductive sinks.

Gibberellins (GA), auxins (IAA), abscisic acid (ABA) and cytokinins (CKs) regulate seed development, with CKs being especially crucial during early seed set, by enhancing sink potential and channeling assimilates toward developing ovaries (4). Increased seed filling in treatments like cycocel, TIBA and paclobutrazol (PCB) can thus be attributed to enhanced source-to-sink translocation (17). The role of B was also evident, as it plays a key part in sugar translocation; its deficiency reduces sucrose and amino acid flow, leading to malformed capitula and poor seed set. Maximum seed setting was observed with 9.38 kg ha^{-1} B, while higher doses produced diminishing returns or adverse effects.

The results indicate that exogenous application of PGRs and B, effectively overcomes seed filling limitations in sunflower by enhancing hormonal activity and assimilate movement from source to sink (Fig. 3) (20). Treatments such as cycocel and B therefore emerged as efficient strategies to increase sink strength and improve seed development, particularly under constrained environments.

PGRs treatments not only improved seed yield attributes but also enhanced oil content, highlighting their dual benefit in sunflower production (3). These findings support earlier evidence that strategies enhancing assimilate partitioning (e.g., cycocel and B) can optimize both yield and seed quality, thereby improving economic returns (21). An increased HI observed in these treatments reflects efficient partitioning of assimilates toward reproductive sinks rather than excessive vegetative biomass accumulation.

By contrast, defoliation experiments-specifically the removal of 33 % basal or middle leaves at the ray floret stage-significantly reduced head diameter, seed filling percentage, seed yield, 100-achene weight, number of achenes per head, TDM and HI (22). Since defoliation was performed before flowering, a stage critical for seed number determination, the reduction in leaf number and area decreased the photosynthetic capacity of plants (23), thereby limiting carbohydrate supply to developing seeds (7). The maximum reduction in yield parameters occurred when middle leaves were removed at the ray floret stage (24), likely because these wider mid-stem leaves contribute 60–80 % of the plant's total photosynthesis and remain active longest after head formation (25). These results reinforce the source limitation concept, where reduced photosynthetic tissue directly constrains sink development and yield.

Overall, the study highlights the importance of integrating PGRs, such as cycocel, with optimized N and micronutrient management to enhance sunflower performance under water-limited conditions. Such combinations improve vegetative balance, strengthen source–sink relationships and enhance assimilate partitioning toward reproductive structures. Conversely, practices that reduce photosynthetic area, such as defoliation, significantly hinder productivity. The findings emphasize that targeted source–sink management through hormonal and nutrient interventions can be a key strategy in developing drought-resilient, high-yielding sunflower hybrids suited for sustainable oilseed production.

Conclusion

The study demonstrated that growth parameters such as plant height, number of leaves, LAD, total leaf area, LAI, SPAD readings and TDM production were significantly influenced by different nutrient and growth regulator treatments across both kharif and rabi seasons. Among these, T8 (double N at sowing + micronutrient mixture at ray floret stage) showed the most consistent and superior performance, followed closely by T7 (foliar humic acid) and T6 (N at star bud stage). These treatments enhanced overall vegetative growth by improving nutrient uptake, chlorophyll retention and leaf expansion. In contrast, treatments involving growth retardants like cycocel (T10), TIBA and BA led to reduced plant height and vegetative growth, likely due to anti-gibberellin effects inhibiting cell expansion. Although cycocel reduced vegetative growth, it showed better seed filling percent, higher 100-achene weight and seed volume, thereby increasing seed yield up to 30 %. Foliar application of humic acid (T7) substantially increased TDM production, contributing to improved biomass accumulation. Combined growth regulator treatments, particularly TIBA with NAA and B sprays, enhanced assimilate partitioning efficiency and seed yield. Overall, the results emphasize that optimizing nutrient supply and hormonal regulation is crucial for balancing vegetative growth and reproductive efficiency, thereby improving sunflower productivity.

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Authors' contributions

TKN contributed to conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, supervision, validation, visualization, writing of the original draft and review and editing of the manuscript. KSS contributed to conceptualization, data curation, formal analysis, methodology, writing of the original draft and review and editing of the manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interest to declare.

Ethical issues: None

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