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RESEARCH ARTICLE

# Genotype × environment interaction and stability of high oleic sunflower (*Helianthus annus* L.) hybrids across temperature regimes

**M.S. Umar Farooq*, M. S. Uma[1], S.D. Nehru[1], Vikas V. Kulkarni[2], B.N. Harish Babu[3] and C. P. Manjula[1]**

## Abstract

Sunflower cultivation in India faces challenges related to environmental variability, particularly in the choice of hybrid varieties for different regions and seasons. This study focuses on the development and stability evaluation of high-oleic sunflower hybrids, emphasizing oleic acid content, which is associated with health benefits. Thirty high-oleic hybrids along with four check hybrids were tested across multiple locations and seasons in Karnataka, India. Analysis of variance using the additive main effects and multiplicative interaction model revealed significant genotype × environment interactions, highlighting the variability in hybrid performance. Promising high-oleic hybrids were identified based on stability across locations and seasons. Interestingly, some hybrids exhibited high oleic acid content during the *rabi*/summer season but not during the *rabi* season, indicating sensitivity to temperature changes. Furthermore, the study explored the influence of climatic variables, confirming that temperature as key factor affecting the oleic acid content. The results emphasized the importance of the *rabi*/summer season for high-oleic sunflower cultivation in India. These findings provide valuable insights for sunflower breeding programs, enabling the development of stable and adaptable high-oleic sunflower hybrids that meet India's agricultural and nutritional demands.

**Keywords:** AMMI, G×E Interaction, Oleic acid content, Temperature, Sunflower hybrids

## Introduction

Sunflower is a photoperiod-insensitive crop, allowing for year-round cultivation. When soil moisture levels are sufficient, optimal seed yields are typically obtained during the *rabi* and *rabi*/summer seasons. However, the *kharif* season, which is favorable for sunflower cultivation, is also susceptible to pests and diseases, posing a threat to crop yields. It's important to note that no single sunflower hybrid is suitable for all regions in India, as sunflowers thrive in varying soil types and require different levels of rainfall. Consequently, hybrid performance varies depending on the specific season and location. This variation is largely attributed to the dynamic production environments characterized by temporal (year-to-year) and spatial (location-to-location) fluctuations, resulting in significant interactions between genotype and year as well as genotype and location, as observed in the study by Vega et al. (2001). Hybrids that consistently perform well across different years and locations are considered stable and adaptable, which is crucial from a commercial crop production perspective. However, it's worth noting that hybrids often exhibit inconsistent performance across different environments due to the genotype-environment interaction (GEI) crossover effect, as discussed by Flores et al. (1998). This significant GEI

Department of Genetics and Plant Breeding, ICRP on Sunflower University of Agricultural Sciences, GKVK, Bangalore 560 065, Karnataka, India.

[1]ICRP on Sunflower University of Agricultural Sciences, GKVK, Bangalore 560 065, Karnataka, India.

[2]AICRP on Sunflower, MARS, University of Agricultural Sciences, Raichur 584 104, Karnataka, India.

[3]AICRP on Groundnut, ZAHRS, Hiriyur 577 598, Karnataka, India.

***Corresponding Author:** M.S. Umar Farooq, Department of Genetics and Plant Breeding, University of Agricultural Sciences, GKVK, Bangalore 560 065, Karnataka, India, E-Mail: umar.gpb@gmail.com

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can hinder the effective selection of superior hybrids, posing a challenge to sunflower breeding and production efforts.

Standard sunflower oil contains approximately 85% unsaturated fatty acids, with linoleic acid being the predominant component, ranging from 44 to 75%, while oleic acid is the least abundant, constituting between 14 and 27%. The US Food and Drug Administration (FDA) found substantial evidence supporting the health claim that oleic acid can reduce the risk of coronary heart disease (US FDA 2018). Consequently, in recent decades, plant breeders have started developing sunflower varieties with significantly elevated oleic acid content, reaching levels of up to 70% or higher. This development has opened up new opportunities for utilizing crops like sunflower, driven by the growing commercial demand for high-oleic oil due to its recognized health benefits (Ramadan et al. 2013).

High-oleic sunflower hybrids exhibit increased susceptibility to temperature fluctuations when compared to standard hybrids (Izquierdo and Aguirrezabal 2008). A combination of major and minor genes influences the stability of the high oleic acid content in these hybrids. Notably, the number of minor genes involved in shaping the high oleic trait can significantly impact a genotype's sensitivity to environmental conditions (Zuil et al. 2012). Even minor fluctuations in oleic acid content within high-oleic hybrids can lead to deviations from the desired high-oleic quality criteria (Echarte et al. 2010). Given that both genotype and environmental factors exert substantial influence over the fatty acid content of sunflowers, it becomes imperative for plant breeders to assess hybrids across diverse growing regions to ascertain their stability. In the context of high-oleic sunflower breeding programs, maintaining the consistency of the oleic acid trait under varying crop growing conditions is paramount. To expedite this process, breeders can employ advanced statistical analysis of yield trials, as advocated by Gauch 1 (2006), enabling more rapid progress in the evaluation of hybrids across different conditions.

Research into high-oleic sunflower hybrids in India has recently gained renewed attention, although progress within the public sector has been somewhat sluggish. Thus far, there have been no reports of successful development of a high-yielding sunflower hybrid with elevated oleic acid content, whether in the public or private sectors. Given this context, the present study was undertaken with the aim of enhancing the quality of sunflower oil through targeted modification of its fatty acid composition. The primary objective has been cultivating high-oleic sunflower hybrids and rigorously evaluating their performance across diverse locations and seasons. The overarching goal is to create high-oleic sunflower hybrids that exhibit high-yield potential and meet consumers' nutritional requirements. This study's central focus revolves around the assessment of stability and adaptability in high-oleic sunflower hybrids across varying environmental conditions and seasonal variations, with a specific emphasis on monitoring oleic acid content.

## Material and methods

### *Planting material and test environments*

This study assessed the stability of 30 high-oleic sunflower hybrids, designated as G1 to G30, each with an oleic acid content exceeding 70% (Table 1). Promising inbred lines

**Table 1.** A list of high oleic hybrids and checks evaluated across environments

| S. No. | Code | Cross Combination | Oleic acid (%) |
|---|---|---|---|
| 1 | G 1 | ARM 249× F-20 | 91.97 |
| 2 | G 2 | CMS 1103A× K-19 | 86.68 |
| 3 | G 3 | CMS 903A× L-11 | 88.75 |
| 4 | G 4 | ARM 249× K-10 | 87.25 |
| 5 | G 5 | CMS 103A× L-3-1 | 86.37 |
| 6 | G 6 | CMS 903A× K-11 | 86.38 |
| 7 | G 7 | CMS 234A× C-30 | 85.87 |
| 8 | G 8 | CMS 234A× K-10 | 88.45 |
| 9 | G 9 | CMS 234A× B-29-2 | 86.30 |
| 10 | G 10 | CMS 1103A× K-11 | 86.10 |
| 11 | G 11 | CMS 903A× N-16 | 86.41 |
| 12 | G 12 | CMS 1103A× G-12 | 85.34 |
| 13 | G 13 | CMS 234A× L-1-1 | 85.20 |
| 14 | G 14 | ARM 249× M-25 | 83.29 |
| 15 | G 15 | CMS 59A× L-11 | 86.40 |
| 16 | G 16 | CMS 234A× L-17 | 82.61 |
| 17 | G 17 | CMS 59A× F-20 | 83.10 |
| 18 | G 18 | CMS 1103A× G-5 | 82.90 |
| 19 | G 19 | ARM 249× L-3-1 | 78.68 |
| 20 | G 20 | ARM 249× K-19 | 77.55 |
| 21 | G 21 | CMS 234A× D-33-2 | 80.62 |
| 22 | G 22 | CMS 234A× D-11 | 76.58 |
| 23 | G 23 | ARM 249× D-11 | 75.51 |
| 24 | G 24 | CMS 903A× G-17-1 | 76.68 |
| 25 | G 25 | CMS 234A× L-3-1 | 75.18 |
| 26 | G 26 | CMS 234A× K-3 | 74.59 |
| 27 | G 27 | CMS 59A× A-16 | 76.68 |
| 28 | G 28 | CMS 1103A× F-20 | 75.81 |
| 29 | G 29 | CMS 903A× B-32-1 | 73.35 |
| 30 | G 30 | CMS 234A× G-12 | 73.37 |
| 31 | C-1 | KBSH-44 | 46.15 |
| 32 | C-2 | KBSH-53 | 38.11 |
| 33 | C-3 | KBSH-78 | 48.08 |
| 34 | C-4 | RSFH-1887 | 58.38 |

C 1-4 = Checks

characterized by high oleic content were carefully crossed with six distinct cytoplasmic male sterility (CMS) lines to create these experimental hybrids. The selection process employed the Smith-Hazel selection index, allowing for the simultaneous prioritization of high oleic content, increased seed yield per plant, and enhanced oil content. Consequently, based on their performance in accordance with the Smith-Hazel selection index, 30 promising high-oleic hybrids, in addition to four commercial checks, were chosen for further analysis to ascertain their stability.

To identify sunflower hybrids with consistent high-oleic traits, a comprehensive field experiment was conducted across two seasons: *rabi*/summer 2020-21 and *rabi* 2021, encompassing three distinct locations in Karnataka, India. These locations included AICRP on Sunflower, GKVK, Bangalore, ZAHRS, Hiriyur, and AICRP on Sunflower, Raichur. The experimental design utilized a randomized complete block design (RCBD) with two replications at each location to ensure the robustness of the results. Climate data for each location is presented in Table 2 for reference. Fatty acid analysis was carried out using gas chromatography (GC) at the Indian Institute of Oilseed Research in Hyderabad.Top of Form

### *Statistical analysis*

Oleic acid content (OAC) data from all test environments were analyzed using the additive main effects and multiplicative interaction (AMMI) method, which integrates analysis of variance and principal component analysis (PCA) divided into two main components by Gollob's F-test (Gollob 1968) into a single analytical framework (Gauch 1988). The AMMI analysis was performed using the windows-based software GEA-R (Genotype × Environment Analysis with R for Windows) version 4.1, developed by CIMMYT, Mexico.

**Table 2.** Climate during *rabi/*summer (December-March) and *rabi* (September-December) seasons of study locations

| Locations | E1<br>GKVK, Bangalore | E2<br>UAS, Raichur | E3<br>ZAHRS, Hiriyur |
|---|---|---|---|
| Altitude (msl) | 923 m | 393 m | 608 m |
| Latitude | 13°4′42.05»N | 16°12′18.53»N | 13°57′16.40»N |
| Longitude | 77°34′44.35»E | 77°19′49.14»E | 76°38′2.79»E |
| *Rabi/*summer 2020-21 | | | |
| $T_{max}$ (°C) | 28.8 ± 2.5 | 33.8 ± 2.8 | 31.3 ± 2.6 |
| $T_{min}$ (°C) | 18.4 ± 1.2 | 20.6 ± 2.4 | 19.1 ± 2.7 |
| RH (%) | 69.0 ± 5.9 | 51.7 ± 9.3 | 64.4 ± 7.7 |
| Rainfall (mm) | 205 ± 28 | 27 ± 5 | 229 ± 27 |
| *Rabi* 2021 | | | |
| $T_{max}$ (°C) | 26.8 ± 0.9 | 30.5 ± 0.7 | 28.9 ± 0.8 |
| $T_{min}$ (°C) | 15.3 ± 1.4 | 17.7 ± 2.5 | 16.0 ± 1.9 |
| RH (%) | 76.0 ± 1.9 | 69.9 ± 7.3 | 74.2 ± 4.6 |
| Rainfall (mm) | 1863 ± 122 | 1141 ± 104 | 1159 ± 79 |
| % increase of temperature in *rabi*/summer as compared to *rabi* | | | |
| Tmax (%) | 7.46 | 10.81 | 8.30 |
| Tmin (%) | 20.26 | 16.38 | 19.37 |

*The values are the average (Tmax, Tmin and RH) or sum (Rainfall) of 2019 to 2021 of particular seasons. The values after ± are the standard deviation of mean/sum.

Oleic acid content from all environments was used to generate a GGE biplot. The GGE biplot is a graphical representation of genotype and environment effects on trait performance based on singular value decomposition (SVD) of the first two principal components (Yan et al. 2000; Yan 2002; Yan and Kang 2003). Random error is ignored in the GGE biplot. GenStat 18th edition software was used to create the GGE biplot. The "which-won-where" pattern of the GGE biplot was used to identify high-oleic sunflower hybrids that perform well in specific environments (Yan et al. 2000; Yan 2002; Yadawad et al. 2023). The GGE biplot can also be used to visualize the relationships between test environments (Cooper et al. 1997) and genotypes (Yan 2001).

To determine the effects of environment and geographical distance on oleic acid content, seed yield, and oil content during the *rabi* and *rabi*/summer seasons, a Mantel test and a partial Mantel test were performed using dissimilarity matrices of the respective variables. Geographic distance was initially estimated based on the experimental locations coordinates using the distm function in the geosphere v. 1.5-18 package with the haversine method to account for the curvature of the Earth. Similarly, the environmental matrix was created using temperature minimum ($T_{min}$ °C), maximum ($T_{max}$ °C), relative humidity (RH%), and Rainfall (RF mm) of the respective seasons using the distm function in the Vegan package with the Euclidean method using the mantel function. The climate variables used in this study were obtained from the station data. The environmental distance matrix was correlated with the distance matrices of oleic acid content, seed yield, and oil content using the mantel partial function with the data standardized and transformed using the Bray-Curtis index. Both Mantel and partial Mantel tests were implemented in R v. 4.3.1 for Windows® using the Vegan v. 2.6-4 package (Oksanen et al. 2020), using 999 permutations with the Spearman rank method.

## Results and discussion

### *Analysis of variance for stability by AMMI model*

The analysis of variance using the Additive Main Effects and Multiplicative Interaction (AMMI) model for oleic acid content yielded insightful findings. It was observed that the Genotype by Environment (G×E) interaction had a significant impact, explaining 61.57% of the total variation during the *rabi*/summer season and 75.48% during the *rabi* season. These results clearly underscored the fact that the performance of the sunflower hybrids exhibited variability across different environmental conditions.

**Table 3.** AMMI analysis of variance tested across three locations during *rabi/*summer 2020-21 and *rabi* 2021

| Source of variation | df | Oleic acid content (%) | | | |
|---|---|---|---|---|---|
| | | *rabi*/summer 2020-21 | | *rabi* 2021 | |
| | | MSS | % contribution | MSS | % contribution |
| G | 33 | 589.5 | 87.56 | 692.3 | 92.11 |
| E | 2 | 261.8 | 2.35 | 42.1 | 0.34 |
| G×E | 66 | 33.9 | 10.07 | 28.3 | 7.54 |
| PCA-1 | 34 | 40.5 | 61.57 | 41.5 | 75.48 |
| PCA-2 | 32 | 26.9 | 38.43 | 14.3 | 24.52 |

Furthermore, the AMMI analysis of variance indicated that the factors of genotypes, environments, and G×E interaction all held high significance concerning oleic acid content in both seasons (Table 3). The significant mean squares associated with different locations suggested that each environment exerted distinct effects on the productivity of the hybrids. Notably, the significant G×E interaction emphasized that the performance of the hybrids varied significantly across the tested environments, signifying changes in their average rankings from one environment to another. This underscores the importance of verifying the performance of each hybrid within specific environmental conditions (including location and season) and highlights the need to consider the influence of the environment when evaluating each hybrid's performance.

### *Genotype-environment interaction and seasonal variability*

In this study, we employed the powerful statistical tool known as the additive main effects and multiplicative interaction (AMMI) model to delve into genotype-by-environment interactions (GEI) within multi-environment trials. This approach offers a comprehensive perspective by simultaneously considering the main effects and interactions of both genotypes (G) and environments (E) (Gauch 1992). The AMMI model computes principal component scores for both G and E, providing a representative summary of GEI (Nowosad et al. 2016). We focused on the visual inspection and interpretation of GEI components using the biplot display of the first interaction principal component axis (IPCA1) scores plotted against hybrid means and environmental means.

Our AMMI analysis unveiled critical insights into the performance of sunflower hybrids across varying environments and seasons. During the *rabi*/summer season, the majority of the tested hybrids exhibited an above-average general mean, with most displaying high oleic acid content ranging from 70 to 80% (Fig. 1a). However, in contrast, during the *rabi* season, most of the hybrids had below-average general means, and only four hybrids exhibited high oleic content exceeding 60% (Fig. 1b). This significant disparity in oleic acid content expression between the two growing seasons can be primarily attributed to variations in temperature, as previous studies have highlighted the sensitivity of oleic acid content to temperature changes.

The findings of Grunvald et al. (2013) and Van Der Merwe et al. (2016) shed light on the relationship between temperature and oleic acid content in sunflower oil, aligning with our study's observations. These studies highlight the critical role of temperature in influencing the composition of fatty acids in sunflower oil, particularly the conversion of oleic to linoleic acid. Grunvald et al. (2013) demonstrated that higher minimum temperatures favor an increase in oleic acid content. This phenomenon is attributed to the temperature-sensitive nature of the fatty acid desaturase enzyme (FAD 2), which is a key player in the conversion of oleic acid to linoleic acid within the fatty acid biosynthesis pathway. When minimum temperatures are elevated, the activity of FAD 2 is enhanced, leading to a higher accumulation of oleic acid and a reduction in linoleic acid. Similarly, Van der Merwe et al. (2016) observed that high temperatures during seed development can decrease linoleic acid and a corresponding increase in oleic acid percentage in sunflower oil. This indicates that temperature conditions during the critical growth stages of sunflower plants directly impact the final fatty acid composition of the oil.

Applying these insights to our study, we can see a clear correlation between temperature conditions and oleic acid content in the sunflower hybrids. During the *rabi* 2021 season, which experienced relatively lower temperatures (Table 2; average maximum temperature of 28.73°C and average minimum temperature of 16.33°C), the hybrids exhibited lower oleic acid content (Table 4). In contrast, the *rabi*/summer 2020-21 season, characterized by significantly higher temperatures, led to a substantial increase in oleic acid content among the majority of the hybrids. This temperature-dependent response in oleic acid content underscores the sensitivity of sunflower plants to temperature fluctuations, particularly during the crucial stages of oil accumulation. It also highlights the potential for environmental conditions to influence the selection of sunflower hybrids for specific purposes. For instance,

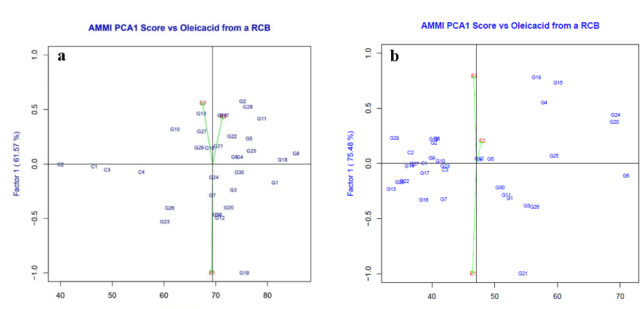


**Fig. 1.** Biplot of oleic acid content means (%) *v/s* IPCA1 for 30 hybrids over three locations during *rabi*/summer 2020-21 (a) and *rabi* 2021 (b)

the hybrids that performed exceptionally well in the *rabi*/summer season may be more suitable for regions or seasons with higher temperature regimes, where the demand for high oleic acid content in sunflower oil is significant.

Our study aligns with previous research, emphasizing the pivotal role of temperature in shaping the fatty acid composition of sunflower oil. Understanding these temperature effects can aid in the strategic selection of sunflower hybrids to meet specific market demands and environmental conditions, ultimately benefiting both farmers and consumers. Further research and field trials in various regions are essential to validate and extend these findings, allowing for more precise sunflower cultivation and oil production recommendations.

Within the AMMI biplot analysis, hybrids with IPCA1 scores close to zero are considered to have undergone minimal interaction effects and are deemed stable across locations. From our analysis (Fig. 1), we identified two stable high oleic hybrids, namely CMS 1103A × G-5 (G-18) and CMS 234A × K-10 (G-8), which exhibited exceptionally high oleic acid content of 82.92 and 85.5%, respectively, across three locations during the *rabi*/summer season (Table 3). These hybrids were positioned with IPCA1 scores very close to zero (Fig. 1a), indicating minimal interaction effects for oleic acid content across the various locations during the *rabi*/summer season. However, it's important to note that these same hybrids did not maintain the same oleic content levels during the *rabi* 2021 season (Table 3), emphasizing their suitability primarily for the *rabi*/summer season (December to March) but not for the *rabi* season (September to December).

In contrast, one hybrid combination, CMS 903A × K-11 (G-6), emerged as a stable high oleic hybrid with a pooled mean of 73.06% oleic acid content across three locations and two seasons (Fig. 1). Identifying this specific hybrid holds significant value as it offers stability in oleic acid content across varying temperature regimes. Nevertheless, further evaluation in diverse regions of India is essential to confirm its adaptability to different temperature regimes and seasons throughout the country. If successful, CMS 903A × K-11 could prove to be a valuable resource for Indian farmers and consumers, addressing both industrial demands and health considerations.

The variations observed in the oleic/linoleic acid ratio can be attributed to the direct effects of temperature on the oleic acid desaturase enzyme (OLD). Elevated temperatures have been shown to reduce the total activity of this enzyme, leading to the storage of oleic acid in triacylglycerols instead of its conversion to linoleic acid (Izquierdo et al. 2013; Dimitrijević et al. 2017). High oleic hybrids, characterized by mutations that reduce the activity of the fatty acid desaturase enzyme, are highly sensitive to temperature fluctuations, unlike traditional check hybrids with lower oleic content (C1 to C4) and higher OLD enzyme activity, which are affected to a lesser extent (Fig. 1). This phenomenon is likely due to the higher abundance of the OLD enzyme in the seeds of traditional check hybrids, resulting in less variation in oleic acid content across different environments compared to high oleic hybrids. Moreover, it is worth noting that traditional check hybrids undergo extensive stability analyses across a wide range of environmental conditions. These rigorous evaluations ensure the consistent and stable expression of traits before these hybrids are approved and released for cultivation. Consequently, the results of the present study demonstrate that the check hybrids consistently exhibit lower oleic content across diverse environments, reaffirming their stability and reliability in this regard.

These findings hold significant practical implications for sunflower cultivation in India. Farmers and breeders need to consider the choice of hybrids based on the specific growing season and the prevailing temperature conditions. High oleic hybrids like CMS 1103A × G-5 (G-18) and CMS 234A × K-10 (G-8) are suitable for the *rabi*/summer season when temperatures are higher, while hybrids like CMS 903A × K-11 (G-6) exhibit stability across seasons and can provide consistent oleic acid content. Sunflower oil with high oleic acid content is not only sought after for its potential health benefits but also for its industrial applications. Identifying stable high oleic hybrids like CMS 903A × K-11 (G-6) holds promise for meeting the nation's nutritional and industrial demands. In conclusion, this study highlights the complex interplay between sunflower hybrids and environmental factors, with a specific focus on temperature and its impact on oleic acid content. The findings contribute to our understanding of the genotype-by-environment interaction in sunflower cultivation, paving the way for more informed decisions by farmers and breeders in selecting hybrids that meet specific seasonal and environmental requirements. Further research and field testing will be essential to fully realize the potential of stable high oleic hybrids across diverse regions of India.

### *Influence of climatic variables*

The Mantel test revealed a significant correlation between geography and climate during both the *rabi*/summer ($r = 0.85$, $p > 0.001$, $n = 102$, 999 runs) and *rabi* ($r = 0.82$, $p > 0.001$, $n = 102$, 999 runs) seasons, indicating that the environmental conditions at the experimental locations varied depending on the season. Therefore, the study further aimed to examine the individual impact of climatic variables on the tested variables, assuming that this would provide insights into the magnitude of the impact. During the *rabi*/summer season, both geographic distance and environment were positively correlated with oleic acid content (OARS), seed yield (SYRS), and oil content (OCRS) (Fig. 2a, Mantel test, $p < 0.01$). However, geographic distance and environment were negatively correlated with OAR, SYR, and OCR during

**Table 4.** Mean Oleic acid content (OAC) of the 30 hybrids tested across three locations over two seasons

| Hybrids | *rabi*/summer2020-21 (December-March) | | | *rabi* 2021 (September-December) | | | *rabi*/summer2020-21 and *rabi* 2021 |
|---|---|---|---|---|---|---|---|
| | OAC (%) | PCA-1 | PCA-2 | OAC (%) | PCAI | PCA II | Pooled mean of OAC (%) |
| G1 | 81.44 | -0.426 | -1.473 | 52.39 | -0.005 | 0.611 | 66.92 |
| G2 | 76.22 | 1.424 | -0.533 | 40.29 | 0.425 | -0.123 | 58.26 |
| G3 | 70.3 | -0.591 | -1.578 | 55.09 | 0.663 | 0.283 | 62.70 |
| G4 | 75.5 | 0.160 | 0.441 | 57.83 | -0.204 | -0.133 | 66.67 |
| G5 | 71.25 | 0.577 | -1.344 | 49.33 | 0.759 | -0.531 | 60.29 |
| G6 | 75.2 | 0.158 | 0.286 | 70.91 | -0.435 | 0.037 | 73.06 |
| G7 | 70.8 | -0.716 | -0.819 | 41.87 | 0.205 | -0.223 | 56.34 |
| G8 | 85.5 | 0.239 | 0.435 | 40.75 | -0.225 | 1.552 | 63.13 |
| G9 | 72.52 | -1.157 | 1.840 | 39.97 | -1.757 | 1.213 | 56.25 |
| G10 | 61.1 | -1.154 | 0.198 | 41.33 | 0.802 | -0.092 | 51.22 |
| G11 | 78.93 | 1.028 | -0.469 | 51.83 | 0.336 | 0.231 | 65.38 |
| G12 | 71.67 | -1.225 | -1.097 | 47.50 | -0.932 | -1.449 | 59.59 |
| G13 | 69.63 | 1.144 | -0.650 | 33.50 | 0.524 | -0.018 | 51.57 |
| G14 | 62.13 | 1.104 | 0.085 | 36.38 | -0.619 | -0.045 | 49.26 |
| G15 | 67.3 | 0.789 | 0.103 | 60.08 | 1.315 | -0.888 | 63.69 |
| G16 | 70.55 | 0.361 | -0.166 | 38.67 | -1.550 | 0.760 | 54.61 |
| G17 | 73.65 | 1.104 | 0.209 | 38.83 | -0.183 | -0.191 | 56.24 |
| G18 | 82.92 | 0.098 | 0.408 | 40.25 | 1.004 | 0.910 | 61.59 |
| G19 | 70.52 | -2.472 | -0.746 | 56.61 | -1.712 | -1.209 | 63.57 |
| G20 | 73.4 | -0.991 | 0.052 | 69.04 | 1.406 | -0.747 | 71.22 |
| G21 | 73.17 | 0.405 | 0.157 | 54.50 | 0.054 | -0.066 | 63.84 |
| G22 | 74.55 | 0.627 | 0.248 | 35.58 | -0.064 | 0.004 | 55.07 |
| G23 | 66.8 | -1.310 | -0.062 | 42.08 | 1.610 | 0.666 | 54.44 |
| G24 | 60.17 | -0.303 | -0.494 | 69.25 | 0.166 | -0.225 | 64.71 |
| G25 | 76.88 | 0.298 | -0.838 | 59.43 | -0.130 | 0.558 | 68.16 |
| G26 | 67.22 | -1.002 | 1.267 | 56.33 | 0.878 | 0.130 | 61.78 |
| G27 | 69.35 | 0.739 | 1.126 | 37.17 | -1.687 | 0.413 | 53.26 |
| G28 | 76.43 | 1.296 | -0.343 | 34.83 | -0.201 | -0.107 | 55.63 |
| G29 | 68.82 | 0.372 | 0.642 | 34.00 | 0.005 | -2.273 | 51.41 |
| G30 | 74.67 | -0.190 | 0.096 | 50.83 | 1.134 | 1.162 | 62.75 |
| C1 | 49.02 | -0.059 | 0.681 | 38.75 | -0.293 | -0.052 | 43.89 |
| C2 | 46.52 | -0.012 | 0.642 | 36.58 | -0.388 | 0.007 | 41.55 |
| C3 | 40.01 | -0.131 | 0.885 | 42.08 | -0.545 | -0.097 | 41.05 |
| C4 | 55.63 | -0.182 | 0.812 | 47.43 | -0.355 | -0.068 | 51.53 |

the rabi season. Similar trends were observed with the partial Mantel test by climate (Fig. 2b), where the *rabi*/summer season registered a significantly positive correlation with OARS, SYRS, and OCRS, while the *rabi* season registered a significantly negative correlation with OAR, SYR, and OCR. We observed a trend that OA and OC had an opposite correlation with SY for both geography and climate distances by the Mantel test, but this was only captured by the partial Mantel test because the geographic distance masked the climate. The proportion of variance explained by the environmental variables by the Mantel test ranged from 1 to 3%, with $T_{min}$ and RH recording the maximum variability, followed by $T_{max}$ and RF. However, the geographic distance was included as a partial Mantel test, and the proportion of variance explained by the environmental variables ranged from 56 to 94% with $T_{max}$ followed by $T_{min}$ and RH recording the maximum variance, followed by RF.

Sunflower productivity, in terms of seed yield, oil, and oleic acid, varies widely depending on environmental factors such as radiation (Dosio et al. 2000), temperature

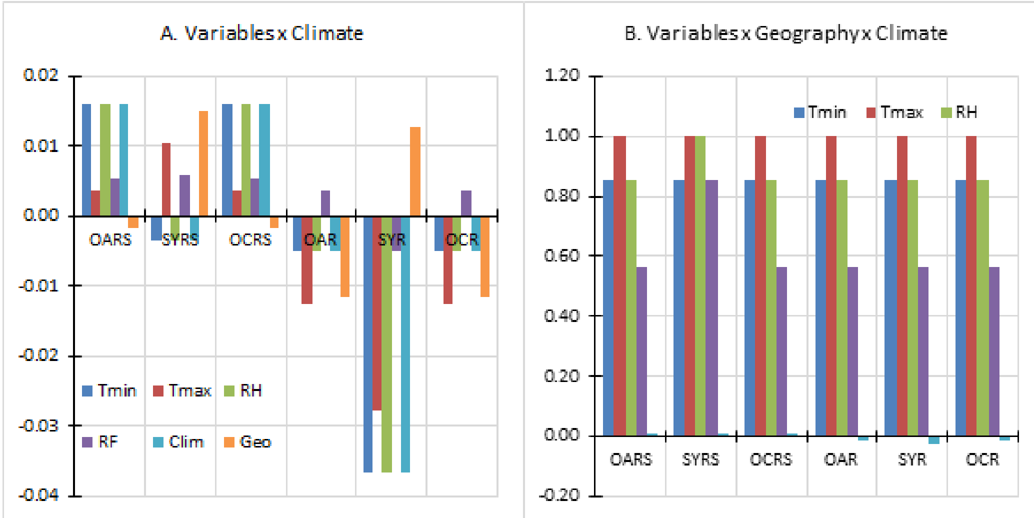


**Fig. 2.** Mantel t-test for oleic acid content (OA), seed yield (SY), and oil content (OC) with climatic variables (A) and its interaction with geography (B) during *rabi*/summer (RS) and *rabi* (R) seasons of 2020-21. $T_{min}$ = Temperature minimum; $T_{max}$ = Temperature maximum; RH = Relative humidity; RF = Rainfall; Clim. = All the climatic variables and Geo. = Geographical distance with altitude

(Sefaoglu et al. 2023; Imerovski et al. 2017; Echarte 1 et al. 2013), and rainfall distribution (Lawal et al. 2011; Olowe et al. 2013). The number of seeds per capitulum, seed weight, and oil concentration determines oil yield per plant. These three components are genetically influenced (Connor and Hall 1997) but can be highly modified by the environment and growth conditions (Bange et al. 1997). Differences in genotypic responses to various environmental variables, specifically maximum and minimum temperature ($T_{max}$ and $T_{min}$), in different experimental seasons may be attributed to the temperature during grain filling time. These results clearly indicate that the variations in the oleic/linoleic acid ratio are explained by the direct effects of temperature on the oleic acid desaturase enzyme. Increasing temperature reduces the total activity of this enzyme, and oleic acid is stored in triacylglycerols instead of being desaturated to linoleic acid (Garcés and Mancha 1991; Garcés et al. 1992). The effect of night temperature on oleic percentages in sunflower genotypes has been reported (Izquierdo et al. 2006; Izquierdo and Aguirrezábal 2008). In this study, the hybrids exhibited high oleic content during the *rabi*/summer season (Fig. 1) which had the higher night temperatures (Table 1). This observation confirms that the 'night' effect appears to be related to increased desaturation from oleic to linoleic acid during the dark period of the daily cycle (Pleite et al. 2008).

### *Test environment evaluation based on GGE biplots*

To gain deeper insights into the relationships among the test environments and their impact on oleic acid content, we employed the environment-vector view of the GGE biplot. This approach enabled us to visualize the interplay between locations and seasons within the multi-location and multi-season trial data. Fig. 3 presents the GGE biplot, revealing the unique characteristics of the evaluated environments. In this context, E1, E2, and E3 correspond to the locations assessed during the *rabi* 2021 season, while E4, E5, and E6 represent the locations evaluated during the *rabi*/summer 2020-21 season. The lines extending from the biplot origin to the test environments are referred to as environment vectors.

A key observation derived from the GGE biplot is the negative correlation between environments associated with the *rabi* and *rabi*/summer seasons, specifically in terms of oleic acid content expression. This negative correlation is visually evident in the biplot, where the environment vectors of locations assessed during the *rabi* season (E1, E2, and E3) align with the negative axis. In contrast, the environment vectors of locations evaluated during the *rabi*/summer season (E4, E5, and E6) align with the positive axis. The insights gleaned from the GGE biplot provide compelling evidence that the *rabi*/summer season, spanning from December to March, emerges as the most favorable season for the cultivation of high-oleic sunflower hybrids. This season exhibits a distinct positive impact on oleic acid content, as indicated by the positioning of environment vectors along the positive axis in the biplot.

In summary, the environment-vector view of the GGE biplot offers a comprehensive perspective on the relationships among test environments, shedding light on the impact of seasonal variations on oleic acid content in sunflower hybrids. The contrasting positioning of environment vectors for *rabi* and *rabi*/summer seasons underscores the seasonal favorability of the latter for the development of high-oleic sunflower hybrids. This valuable insight can inform cultivation practices and breeding strategies to maximize oleic acid content in sunflower crops, ultimately enhancing the quality of sunflower oil production.

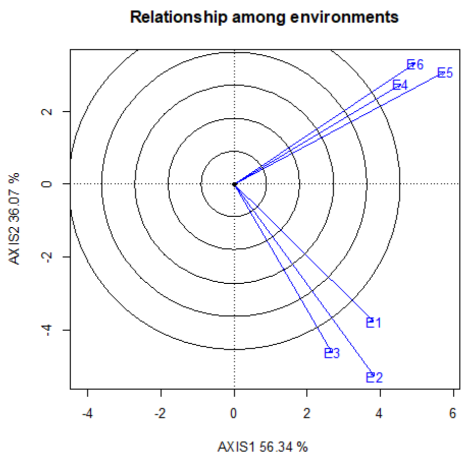


**Fig. 3.** The environment-vector view of the GGE biplot for oleic acid content to show similarities among test environments in discriminating the hybrids over both *rabi*/summer 2020-21 and *rabi* 2021 seasons combined

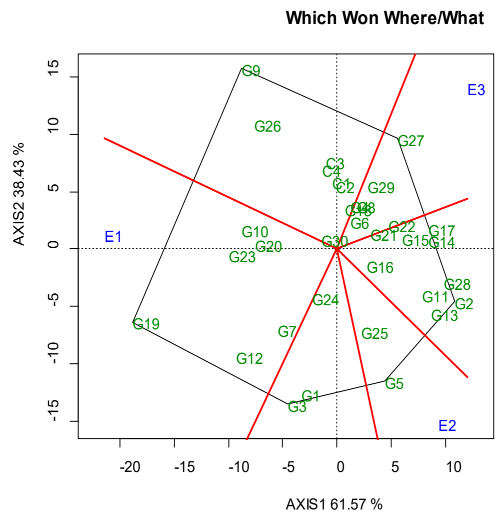


**Fig. 4.** The which-won-where view of the GGE bi-plot to show which hybrids performed well in which environments for Oleic acid content during *rabi*/summer 2020-21

### *Which Won Where*

A notable advantage of the GGE biplot lies in its ability to illustrate the "which-won-where" pattern within a genotype by environment dataset, as depicted in Fig. 4. This aspect of the biplot analysis is highly regarded by researchers (Yan 2011; Olivoto et al. 2019; Choudhary et al. 2019) due to its capacity to visually convey essential concepts like crossover genotype-environment interactions (GEI), mega-environment differentiation, and specific adaptation. To create the which-won-where graph, a polygon is initially constructed using the genotypes situated furthest from the biplot origin. This ensures that all additional genotypes fall within the polygon. Perpendicular lines are then drawn from the biplot origin to each side of the polygon, enabling the identification of genotypes located at the polygon's vertices. These corner genotypes are crucial because they either excelled or underperformed in one or more environments.

Specific test hybrids stand out as top performers in particular environments in the which-won-where view of the GGE biplot for oleic acid content (Fig. 4). For instance, test hybrid G19 demonstrated exceptional suitability in E1 (Bangalore) by exhibiting the highest oleic acid content among all test hybrids within this environment. Similarly, test hybrids G-5 and G-27 showcased superior performance for oleic acid content in E2 (Raichur) and E3 (Hiriyur), respectively, outperforming their counterparts in these specific environments.

In summary, the which-won-where view of the GGE biplot serves as a valuable tool for pinpointing top-performing hybrids in specific environments. This graphical representation enables researchers to identify genotype-environment interactions, thereby facilitating informed decisions for crop breeding and cultivation practices that maximize performance and adaptability in diverse environmental conditions.

## Authors contributions

Conceptualization of research (MSUF, UMA); Designing of the experiments (UMA, NSD, MCP); Contribution of experimental materials (VK, HB); Execution of field/lab experiments and data collection (MSUF); Analysis of data and interpretation (MSUF); Preparation of the manuscript (MSUF).

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