



# Genotype–Trait Interaction Analysis in Camelina Doubled Haploid Lines Using the GGE Biplot Method

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## ABSTRACT

Camelina (*Camelina sativa*), an oilseed crop with high-quality oil, holds significant potential for food and biofuel production. Identifying high-yielding, stable genotypes is key for camelina breeding in dryland conditions. This study used the genotype-trait (GT) biplot method to explore trait relationships in camelina doubled haploid (DH) lines. Fifteen DH lines and Soheil variety were assessed in Gonbad-e Kavous under dryland conditions using a randomized complete block design with three replications in 2022. Traits including days to maturity, plant height, branching height, number of sub-branches, number of pods on the main branch, number of pods on the sub-branch, number of pods per plant, number of seeds per pod, thousand-kernel weight, seed yield, oil content, and oil yield were measured. The GT biplot accounted for 53% of total variance, with the first and second principal components explaining 28.2% and 24.8%, respectively. The GT biplot's polygonal representation identified G1 and G8 as the top genotypes for seed yield, oil yield, plant height and branching height traits. The GT biplot analysis showed positive correlations between seed and oil yields with plant height, branching height, number of pods on the sub-branch, the number of pods per plant, and the number of seeds per pod. Selecting these traits is expected to enhance seed and oil yields, which were positively correlated, whereas the association between seed yield and thousand-kernel weight was weak. The traits closest to the hypothesized ideal were the number of seeds per pod, number of pods per plant, number of pods on the sub-branch, and branching height. G15, G13, G5, and G1 were the most desirable across all evaluated traits, while G10 and G11 were the least favorable. G15 and G13 showed the greatest stability. Trait-based selection plays a crucial role in enhancing seed and oil yields in camelina breeding programs under dryland conditions.

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## 1. Introduction

Camelina (*Camelina sativa* L.), a member of the Brassicaceae family (Berti *et al.*, 2016), is an industrial oilseed crop valued for its versatility and potential in biofuel production, food, and feed applications (Masella *et al.*, 2014). Data on the global Camelina cultivation area remains limited. However, Camelina farming has experienced significant expansion, with 65,000 acres contracted in 2023 across the United States, South America, and Europe. In Iran, the

cultivated area reached approximately 20,000 hectares during the 2022–2023 growing season, highlighting its growing importance in agricultural development. Compared to other oilseed crops such as canola (*Brassica napus*) and sunflower (*Helianthus annuus*), camelina exhibits superior resource-use efficiency and environmental adaptability (Zanetti *et al.*, 2021; Wang *et al.*, 2022). The shift toward sourcing omega-3 fatty acids from plant-based rather than animal-based origins has heightened interest in camelina, given its high

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omega-3 fatty acid content (Toncea et al., 2013). Additionally, Camelina exhibits notable agronomic advantages, particularly its rapid growth cycle, reaching maturity within approximately 85 to 100 days (Ghidoli et al., 2023). Camelina has relatively low fertilizer requirements and demonstrates greater adaptability to water-limited environments compared to other oilseed crops like canola or sunflower (Obour et al., 2015; Rostami Ahmadvandi and Faghihi, 2021). It serves as a viable option to replace fallow periods in dryland cereal-based cropping systems, particularly in semiarid regions (Obour et al., 2017). Additionally, the crop displays resistance to major pathogens and insect pests that commonly affect other Brassicaceae species, such as oilseed rape (Tepfer et al., 2020). However, due to its limited cultivation and neglect over the past century, existing cultivars have not significantly benefited from recent advances in plant breeding (Tepfer et al., 2020). As a result, there is a pressing need to develop high-yielding genotypes to realize camelina's agricultural potential. Doubled haploid (DH) technology has emerged as a valuable tool in this regard, enabling the rapid generation of homozygous lines (Soorni et al., 2022; Chen et al., 2024). This approach has been successfully implemented across numerous plant species to accelerate the development of pure lines with improved traits (Shahadati-Moghaddam et al., 2016). In camelina breeding, the identification of high-yielding genotypes is of paramount importance. Precise evaluation of genotypes across various traits is essential for identifying ideal candidates for breeding programs.

A robust statistical tool for analyzing trait correlations, assessing genotypes across multiple traits, and pinpointing individuals that excel in specific characteristics is the genotype–trait (GT) biplot analysis. This method provides a comprehensive and visual representation of complex interactions between genotypes and traits, enabling breeders to make informed decisions and prioritize genotypes with superior performance (Stansluos et al., 2023). The GT biplot, a component of the GGE biplot methodology, is specifically designed to investigate the relationships between genotypes and traits, providing insights into how specific traits influence genotype performance (Mousavi et al., 2021). The GT biplot method has been widely applied to investigate genotype  $\times$  trait correlations in various crops, including maize

(Mousavi et al., 2021; Stansluos et al., 2023), wheat (Akcura and Kokten, 2017), sunflower (Shojaei et al., 2022), cowpea (Adedeji et al., 2020), cotton (Xu et al., 2017). In this study, camelina doubled haploid lines and the Soheil cultivar was examined. The primary objectives were to: (1) evaluate the genotype  $\times$  trait interaction effects and analyze the correlations among the studied traits and their interrelationships; (2) identify DH lines with the most desirable traits; and (3) classify the DH lines based on the studied traits using the GT biplot technique.

## 2. Materials and methods

Fifteen advanced doubled haploid (DH) lines of camelina, along with the Soheil variety (control), were cultivated in a randomized complete block design (RCBD) with three replications at the National Agricultural Research Station and Dryland Seed Production in Gonbad-e Kavous, northern Iran, during the 2022 cropping season. These lines were developed via anther culture and provided by the Shafa Biston Co., Iran. The names and codes of the camelina DH lines included in the experiment are detailed in Table 1. Seeds of each genotype were manually planted in rows, with each experimental plot covering an area of 6 m<sup>2</sup>, consisting of four rows spaced 25 cm apart. The genotypes were evaluated under dryland spring cultivation conditions. Geographical and meteorological details of the experimental site are summarized in Table 2, while the soil characteristics of the experimental site are outlined in Table 3.

**Table 1. Names and code of camelina doubled haploid (DH) lines evaluated in the experiment**

Number	Genotype code	Genotype name	Number	Genotype code	Genotype name
1	G1	DH60	9	G9	DH107
2	G2	DH61	10	G10	DH128
3	G3	DH105	11	G11	DH200
4	G4	DH40	12	G12	DH15
5	G5	DH20	13	G13	DH82
6	G6	DH100	14	G14	DH41
7	G7	DH114	15	G15	DH69
8	G8	DH38	16	G16	Soheil*

\*Genotype No. 16, the Soheil cultivar, is considered as the control

**Table 2. Geographical and climatic specifications of the experimental site.**

Location	Longitude	Latitude	Elevation (m)	Average Annual rainfall (mm)	Annual evaporation (mm)
Gonbad/Iran	55°13'E	37°16'N	41	400	1511.9

**Table 3. Soil physiochemical properties of the field area at the National Agricultural Research Station and Dryland Seed Production, Gonbad-e Kavous, northern Iran**

Texture	Potassium (mg.kg <sup>-1</sup> )	Phosphorus (mg.kg <sup>-1</sup> )	Nitrogen (%)	Organic carbon (%)	Calcium carbonate (%)	EC (dS.m <sup>-1</sup> )	pH (1:5)
Silt loam	350	9	0.15	1.46	20	0.73	8.1

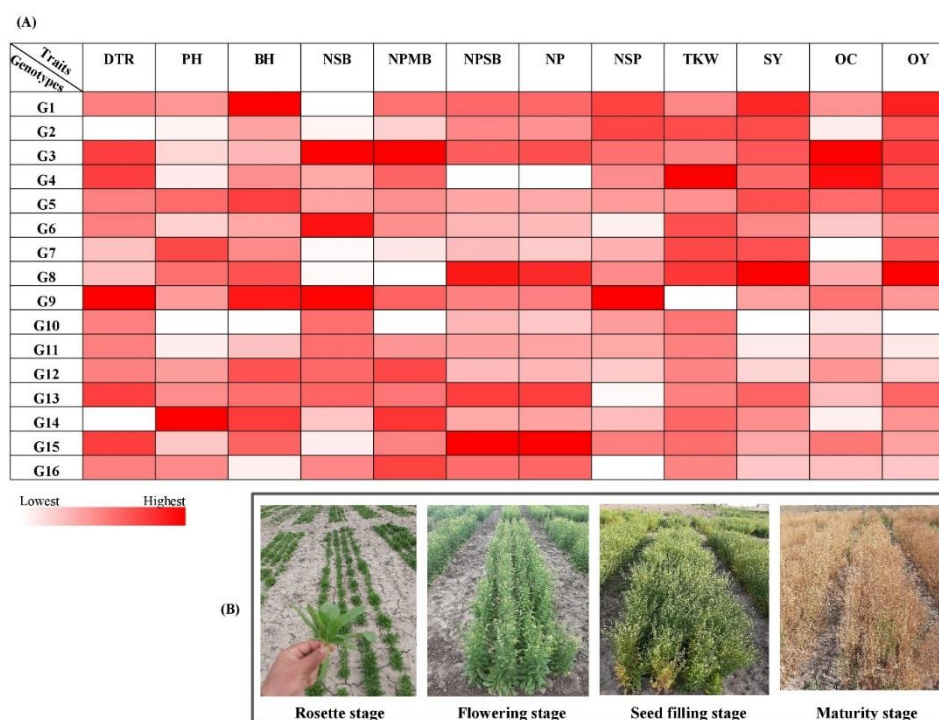
The phenological and agronomic traits measured were days to ripening (DTR), plant height (PH, cm), branching height (BH, cm), number of sub-branches (NSB), number of pods on the main branch (NPMB), pods on the sub-branch (NPSB), pods per plant (NP), seeds per pod (NSP), thousand-kernel weight (TKW, gr), seed yield (SY, kg ha<sup>-1</sup>), oil content (OC, %), and oil yield (OY, kg ha<sup>-1</sup>). The biplot was generated using the GGE biplot software, relying on the first two principal components (PC1 and PC2). Graphical decomposition was performed using a GT biplot for each quantity, as described in Equation 1 (Yan and Rajcan, 2002).

$$(1) \quad \frac{\alpha_{ij} - \beta_j}{\sigma_j} = \sum_{n=1}^2 \lambda_n \xi_{in} \eta_{jn} + \varepsilon_{ij} = \sum_{n=1}^2 \xi_{in}^* \eta_{jn}^* + \varepsilon_{ij}$$

In this research, five GT biplot diagrams were generated: Polygon diagrams for the selection of high-performing genotypes for specific traits, Traits vector view to determine the ideal trait, trait correlations diagram to show inter-trait relationship, ideal genotype diagram to rank genotype against an ideal benchmark, and the stability diagram to assess genotypes stability across traits.

### 3. Results and discussion

The heat map visualization of 16 camelina genotypes was generated based on multiple traits is shown in Fig. 1A. The Heat Mapper tool, known for its user-friendly interface and dynamic, flexible visualization capabilities (Stansluos *et al.*, 2023), was utilized for this purpose. Fig. 1B illustrates key growth stages observed in the camelina DH lines, including the rosette, flowering, seed filling, and maturity.



**Figure 1. Heatmap of morphological and yield-related traits (A) and key growth stages (B) in camelina doubled haploid lines. Heatmap color intensity represents relative trait scale (light red = low; dark red = high). Abbreviations: DTR, days to ripening; PH, plant height; BH, branching height; NSB, number of sub-branches; NPMB, number of pods on main branch; NPSB, number of pods on sub-branch; NP, number of pods per plant; NSP, number of seeds per pod; TKW, thousand-kernel weight; SY, seed yield; OC, oil content; OY, oil yield; G, genotype code.**

#### 3.1. Identification of superior genotypes based on evaluated traits

According to the polygon view of the GT biplot (Fig. 2), the first principal component (PC1) accounted for

28.2% of the variation, while the second principal component (PC2) explained 24.8%. Collectively, these two components explained 53% of the total variation in the dataset. The genotypes positioned at the vertices of

the polygon in the biplot are considered the most superior for the traits situated within the sector defined by the lines extending from the origin to those vertices (Porkabiri et al., 2019). Specifically, the number of traits within a sector correlates with the performance of the genotypes in that sector, with genotypes in sectors encompassing more traits demonstrating superior performance across a broader range of characteristics. Among the DH genotypes, G9, G1, G8, G7, and G10 were positioned at the vertices of the polygon. Genotypes G1 and G8 were identified as the most favorable for seed yield, oil yield, plant height, and branching height (Fig. 2). In contrast, G9 and G3 were optimal for oil content, days to ripening, number of pods on the main branch, and number of sub-branches. While G7 genotype was distinguished as the most suitable for thousand-kernel weight compared to the others. Conversely, the G10 genotype, despite its vertex position, did not demonstrate outstanding performance for any measured traits.

Based on the biplot analysis, five distinct groups were identified, and the 16 DH lines under investigation were classified into four groups. The first group, comprising vertex genotype G7, along with G2 and G14, demonstrated success solely in terms of thousand-kernel weight. The second group, which includes genotypes G1 and G8 at the vertices of the polygon, as well as G5, exhibited success in four key traits: seed yield, oil yield, plant height, and branching height. The inclusion of two critical traits—seed yield and oil content—in this sector highlights the superior performance of these genotypes in terms of seed and oil production. The third group did not include any genotypes within its respective sector, indicating that the measured traits—number of pods on the sub-branch, number of seeds per pod, and number of pods per plant—were not outstanding for any of the genotypes. In the fourth group, genotype G9 at the vertex of the polygon, along with G3, G13, and G15, showed success in four traits: oil content, number of pods on the main branch, number of sub-branches, and days to ripening. The fifth group, containing vertex genotype G10 alongside G4, G6, G11, G12, and G16, did not exhibit success in any of the evaluated traits. The identification of superior genotypes based on assessed traits has been reported for various crops, such as Egyptian broomrape weed (Porkabiri et al., 2019) and maize (Stansluos et al., 2023). A genotype can be

viewed as a collection of traits; therefore, its evaluation should consider multiple traits that align with breeding objectives (Yan, 2014). Both oil content and seed yield are complex traits influenced by various morphological and physiological factors that interact throughout the plant's growth and development cycle, from planting to harvest (Göre and Kurt, 2021).

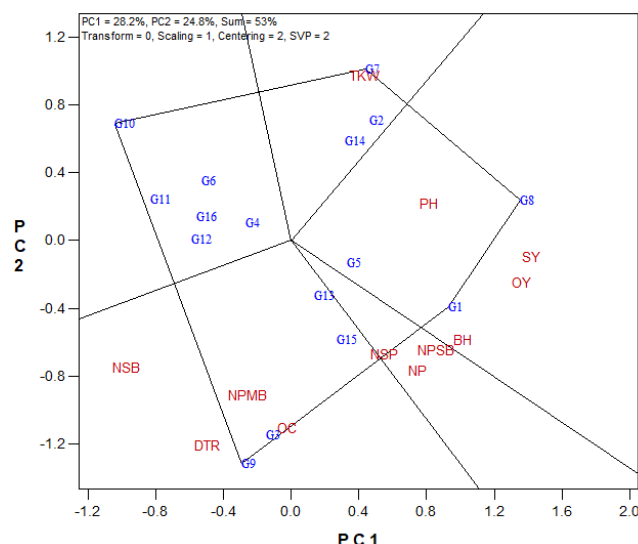
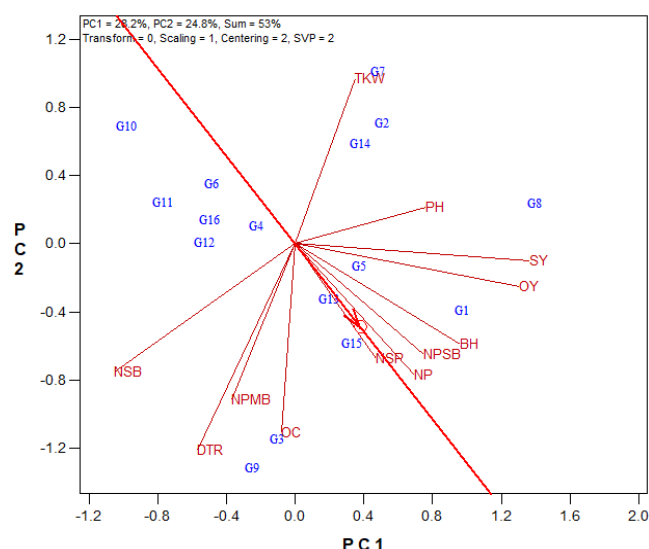


Figure 2. GGE biplot analysis and display of which-won-where pattern based on traits to determine the superior camelina doubled haploid lines. Abbreviations: DTR, days to ripening; PH, plant height; BH, branching height; NSB, number of sub-branches; NPMB, number of pods on the main branch; NPSB, number of pods on the sub-branch; NP, number of pods per plant; NSP, number of seeds per pod; TKW, thousand-kernel weight; SY, seed yield; OC, oil content; OY, oil yield; G, genotype code.

### 3.2. The GT biplot for determining the ideal trait

An ideal trait is defined as one that effectively represents other traits in the study and demonstrates the highest capacity to differentiate among genotypes (Rahimi et al., 2019). Traits are evaluated and ranked based on their proximity to a hypothetical ideal trait. The angle formed between the vector of each trait and the mean trait axis (horizontal axis) serves as an indicator of the trait's representativeness. A smaller angle indicates greater representativeness, signifying that the trait is more representative of the others (Yan and Kang, 2002). In this study, the number of seeds per pod was identified as the trait closest to the hypothesized ideal trait. Subsequently, the number of pods per plant, the number of pods on the sub-branch, and branching height were the next most representative traits, positioned closest to the ideal trait (Fig. 3). The methodology for identifying such ideal traits to select superior genotypes has been previously documented in the context of maize hybrids by Mousavi et al. (2021).



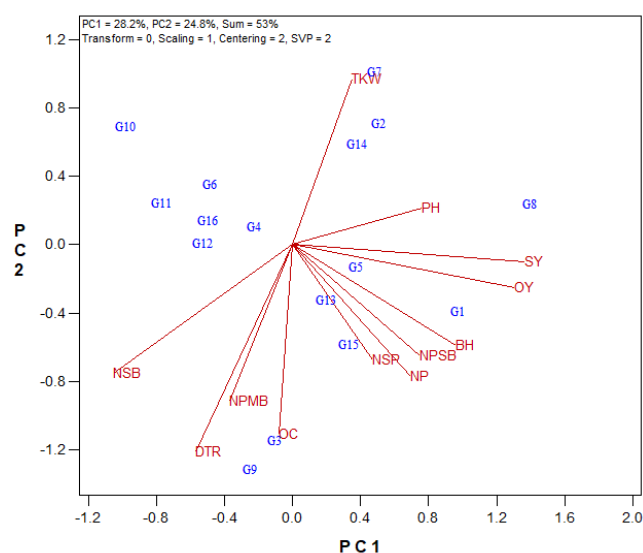


**Figure 3.** GT biplot analysis identifying ideal traits in camelina doubled haploid lines under dryland conditions. Key elements: thick red arrow = mean trait axis (reference line); red circle =hypothetical ideal trait position; narrow red vectors = trait orientation; genotypes markers in blue. Abbreviations: DTR, days to ripening; PH, plant height; BH, branching height; NSB, number of sub-branches, NPMB, number of pods on the main branch; NPSB, number of pods on the sub-branch; NP, number of pods per plant; NSP, number of seeds per pod; TKW, thousand-kernel weight; SY, seed yield; OC, oil content; OY, oil yield; G, genotype code.

### 3.3. Correlations between traits

The strength of correlations between traits is illustrated in Fig. 4, where the angles between trait vectors were used to determine these relationships. When the angle between the vectors of two traits is below 90 degrees, it signifies a positive correlation between them. An angle of exactly 90 degrees indicates no correlation, while an angle greater than 90 degrees suggests the absence of a correlation (Ma et al., 2004). According to the GT biplot vector representation, the traits of plant height and branching height showed the strongest positive correlation with seed yield and oil yield. This was followed by the traits of the number of pods on the sub-branch, the number of pods per plant, and the number of seeds per pod, which also demonstrated positive correlations with seed yield and oil yield (Fig. 4). Consequently, selecting for these traits is anticipated to enhance both seed and oil yields. To develop high-performing genotypes, it is essential to identify genotypes that exhibit favorable values for the aforementioned traits. A positive correlation exists between seed yield and oil yield, a finding that aligns with the research conducted by Vollmann et al. (2007) and Zanetti et al. (2017). However, the relationship between seed yield and thousand-kernel weight was found to be weak, suggesting that seed weight may

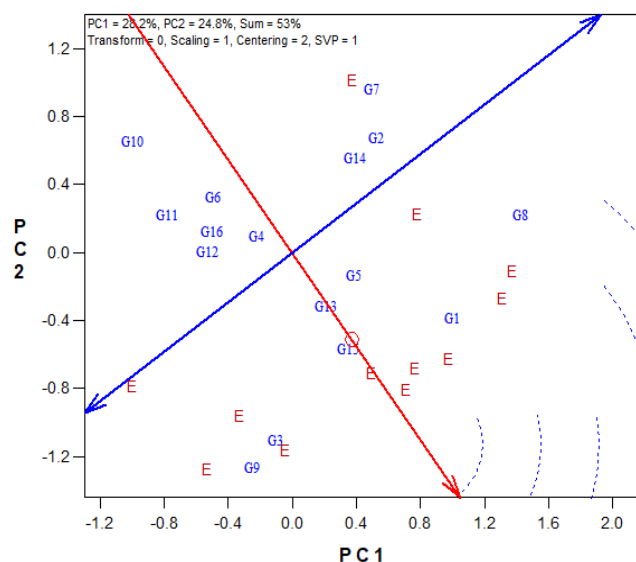
have limited utility as a predictor of seed yields in camelina. This observation is consistent with the results reported by Vollmann et al. (2007) and Obour et al. (2017). This is probably due to the low thousand-kernel weight of camelina. The present study recorded a thousand-kernel weight as high as 1.26 g, which falls within the reported range of thousand-seed weights for camelina, spanning from 0.80 to 1.81 g (Vollmann et al., 2007; Solis et al., 2013; Obour et al., 2017). Zanetti et al. (2017) recently demonstrated that newly enhanced camelina lines, distinguished by their increased seed weight, exhibited higher seed yields compared to lines with average seed weight while maintaining comparable seed oil content. Additionally, traits such as the number of pods on the main branch and the number of days to ripening showed a positive correlation with oil content percentage. Consequently, doubled haploid lines with a longer ripening period tended to have higher oil content. This phenomenon may be attributed to an extended growth period and an increased rate of photosynthate remobilization during the latter stages of the growth cycle, as suggested by Soorni et al. (2022). Furthermore, a negative relationship was observed between thousand-kernel weight and the number of days to ripening, which is consistent with the findings reported by Soorni et al. (2022).



**Figure 4.** GT biplot analysis of 15 camelina doubled haploid lines and Soheil cultivar, showing inter-trait correlations via vector geometry (red lines). Abbreviations: DTR, days to ripening; PH, plant height; BH, branching height; NSB, number of sub-branches, NPMB, number of pods on the main branch; NPSB, number of pods on the sub-branch; NP, number of pods per plant; NSP, number of seeds per pod; TKW, thousand-kernel weight; SY, seed yield; OC, oil content; OY, oil yield; G, genotype code.

### 3.4. Determining the ideal genotype

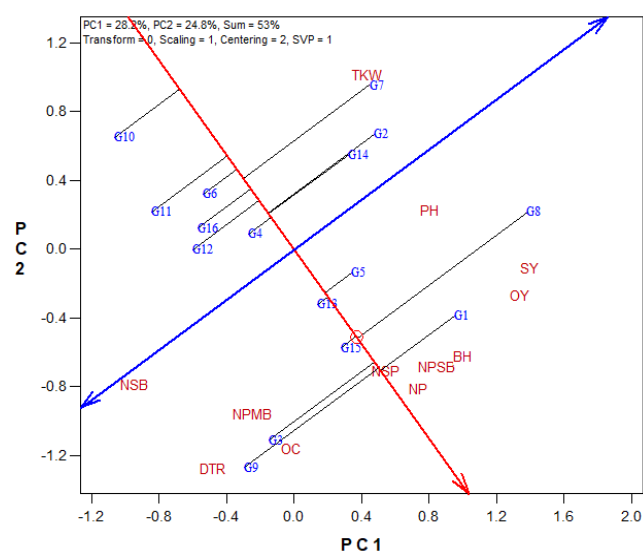
The biplot illustrating the comparison of all genotypes with the ideal genotype is presented in Fig. 5. As defined by Porkabiri et al. (2019), ideal genotypes are characterized by extremely large PC1 scores, indicating high trait means, and small absolute PC2 scores, reflecting low variability. The red circle positioned on the mean trait axis (red axis) represents the hypothetical ideal genotype. While such an ideal genotype does not exist in practice, it serves as a benchmark for ranking other genotypes (Yan and Kang, 2002). DH lines that are positioned closest to the red circle, relative to the ideal genotype, are considered superior across all evaluated traits. Genotypes that are closest to the hypothetical ideal genotype are regarded as favorable across all traits evaluated. In this study, genotypes G15, G13, G5 and G1 were found to have the least distance from the hypothetical ideal genotype and are considered the most desirable genotypes in terms of all traits. According to this biplot, genotypes G10 and G11 were determined to be the least desirable genotypes in comparison to the ideal genotype across all assessed traits. The evaluation of genotypes according to the ideal genotype in camelina (Subaşı et al., 2021), sunflower (Shojaei et al., 2022), and sweet corn (Stansluos et al., 2023) have also been reported.



**Figure 5.** Biplot analysis for ranking 15 camelina doubled haploid lines and Soheil cultivar based on the ideal genotype under dryland conditions, indicating which genotypes were closest to the ideal genotype. The red circle marks the hypothetical ideal genotype. Abbreviations: DTR, days to ripening; PH, plant height; BH, branching height; NSB, number of sub-branches; NPMB, number of pods on the main branch; NPSB, number of pods on the sub-branch; NP, number of pods per plant; NSP, number of seeds per pod; TKW, thousand-kernel weight; SY, seed yield; OC, oil content; OY, oil yield; G, genotype code.

### 3.5. Ranking of genotypes based on stability

The ranking of 16 camelina genotypes based on seed yield and stability is illustrated in Fig. 6. A vertical line, perpendicular to the average environmental performance line, divides the doubled haploids into two groups: those positioned on the right exhibit an average performance exceeding the overall mean, while those on the left show an average performance below the overall mean. Stability, combined with mean useful performance, has proven advantageous, and the GGE biplot method transforms this into a visually assessable criterion (Saeidnia et al., 2023). Among the doubled haploids, G15 and G13 display the highest stability, whereas G5 and G1 fall within the group of doubled haploids exhibiting average stability. In contrast, doubled haploids G8, G9, and G3 demonstrate significant yield fluctuations and are therefore classified as less stable. Similar rankings of genotypes based on stability have been reported in sunflower (Shojaei et al., 2022).



**Figure 6.** Biplot of environmental performance means for ranking camelina doubled haploid lines based on stability. Abbreviations: DTR, days to ripening; PH, plant height; BH, branching height; NSB, number of sub-branches; NPMB, number of pods on the main branch; NPSB, number of pods on the sub-branch; NP, number of pods per plant; NSP, number of seeds in a pod; TKW, thousand-kernel weight; SY, seed yield; OC, oil content; OY, oil yield; G, genotype code.

## 4. Conclusion

This study employed genotype–trait (GT) biplot analysis to evaluate 15 doubled haploid camelina lines and the Soheil under dryland conditions. Through a comprehensive analysis, significant correlations among various morphological and agronomic traits were identified, offering valuable insights for camelina breeding programs. The results highlighted that

architectural traits (plant height, branching height) and reproductive components (number of pods on the sub-branch, number of pods per plant, and number of seeds per pod) were positively correlated with both seed yield and oil yield. Biplot analysis revealed genotypes G15, G13, G5, and G1 as closest to the ideal genotype, demonstrating superior performance across all evaluated traits, while genotypes G10 and G11 were least desirable. Stability analysis based on seed yield identified genotypes G15 and G13 as the most stable genotypes, whereas genotypes G8, G9, and G3 showed significant yield fluctuations, indicating lower stability. The GT biplot method proved to be an effective tool for identifying high-yielding and stable camelina genotypes with potential tolerance to drought stress in semi-arid regions. These findings can inform the development of improved breeding strategies and the selection of suitable methods for advancing camelina genotypes with enhanced agronomic performance. Future research should validate these findings under diverse environmental conditions to further strengthen the robustness and applicability of the breeding program.

### Conflict of interests

All authors declare no conflict of interest.

### Ethics approval and consent to participate

No humans or animals were used in the present research. The authors have adhered to ethical standards, including avoiding plagiarism, data fabrication, and double publication.

### Consent for publications

All authors read and approved the final manuscript for publication.

### Availability of data and material

All the data are embedded in the manuscript.

### Authors' contributions

Hossein Ahmadi-Ochtapeh: Project administration, Methodology, Writing - review & editing, Supervision. Hossein Rostami Ahmadvandi: Provision of genetic materials and scientific consultation throughout project implementation. Abdol Aziz Haghighi: Assistance in the implementation of the project. Masoumeh Kheirgoo: Data collection.

### Informed consent

The authors declare not to use any patients in this research.

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